THE BREEDING CYCLE IN THE BANK SWALLOW

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THE BEHAVIOR of birds during a considerable part of the year is dominated by activities directly related to reproduction. It is not strange that such striking sequences of behavior recurring annually in the lives of birds have long held the interest of man. Only recently, however, have refined techniques of observation been developed which can be applied to field studies of natural behavior.

A general relationship has long been recognized between morphological changes in the reproductive organs and the orderly progress of the breeding cycle in birds. General summaries of these relationships together with interpretations of their endocrinological mechanisms have been provided by Marshall (1929), Huxley (1932), and Groebbels (1937). More detailed work on gonadal recrudescence in relation to breeding activity has been reported for various species by Blanchard (1941), Höhn (1947), Marshall (1951, 1952*a,b,c*) and others, and many workers have investigated the development of the reproductive structures in relation to environmental factors (Burger, 1949; Farner, 1950). Extensions of these descriptive studies to include various aspects of blood chemistry have been made for domestic pigeons and doves by Riddle and his associates (Riddle, 1937*a*; Schooley, 1937; and Riddle, 1942). Experimental investigations of the relationships between breeding behavior and physiology have been reviewed by Bullough (1945), Beach (1948), and Collias (1950).

The purpose of this study is to examine certain aspects of the behavioral and physiological cycles of a wild species for correlations that might shed light on the physiological regulation of natural breeding behavior. This study was carried out in the vicinity of Madison, Wisconsin, during the years 1950 through 1953 and was submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Wisconsin.

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The Bank Swallow as a Subject for Study

The Bank Swallow (*Riparia riparia*) was selected as the subject for this study of breeding cycles for several reasons. The species breeds in easily located colonies of up to several hundred pairs and is common in the vicinity of Madison. The nests are built in burrows which are usually readily accessible and from which the birds can easily be collected. Behavioral characteristics of special interest include a sharing of many of the breeding activities of the two sexes, a long period of nestling development, and a fairly close synchrony of activities within a colony.

Difficulties were presented by the closed nature of the nests, screening many of the breeding activities from view. The similarity of the sexes in appearance and behavior and the concentrations of many pairs in a closely-nesting colony made individual recognition difficult. Finally, the small size of the species placed severe restrictions on the chemical studies and necessitated special techniques.

Previous studies of Bank Swallow behavior provided a background of information helpful in the planning and interpretation of my work. The most extensive of these are Stoner's observations of colony composition and Beyer's (1938) observations of activity within the nest chamber from a darkened pit dug behind the burrow. A number of observations reported for the species in England, where it is called the Sand Martin, are noted below. In none of these were techniques for recognition of individual birds used and sex was known only by dissection.

I. Behavior Cycle of the Bank Swallow

Procedures in Behavior Observations

As many colonies of Bank Swallows as possible were located in Dane County, Wisconsin. Specimens for morphological and physiological studies were collected at certain of the colonies; other colonies were left undisturbed for behavior studies. Collection and autopsy procedures will be described beyond.

Observations of the behavior cycle were made principally at a colony on Nine Springs Creek, two miles south of Madison. The creek is a temporary stream which has eroded a bank in a pastured meadow on the Alfred Keller farm. An observation blind protected by an electric fence from trampling by cows was placed 15 feet from the bank, affording a clear view of nearly

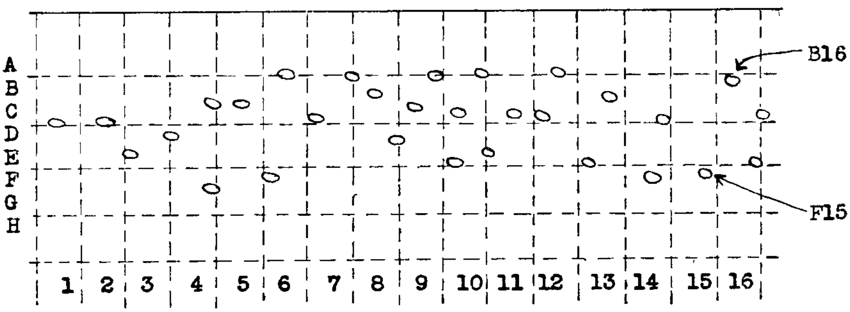

FIG. 1. Map of Bank Swallow burrow entrances illustrating the method of identifying burrows.

all of the burrow entrances. The bank was only six feet high, so the burrows were easily accessible for observation of their interiors and for trapping of the occupants. I attempted to keep the disturbance of my activities at the necessary minimum, and there was no other human interference at this colony.

Individual burrows were identified and designated on a scale map of the burrow entrances with the help of a grid overlay, giving each burrow a letter and a number identification (Fig. 1). Mimeographed copies of this colony map were used for recording observations.

Birds were captured for marking by a method described by Morris (1942). Transparent plastic bags (quart-size frozen food bags) were held by a rubber band over one end of a roll of cardboard and the other end of the cardboard fitted into the burrow entrance. These traps were usually placed just before dawn but were also used with success at various times of day.

The captured birds were individually marked by painting the outer one-inch of the outer or ninth primary feather with airplane dope. The tips of the seventh and eighth primaries were clipped off to completely expose the color marks. Thus, each bird was given a combination of two colors which became its name (for example: left wing-tip orange, right wing-tip red, was abbreviated *OR*).

Sex was determined by presence of a brood patch in females and absence of a brood patch in males.

Eleven broods of nestlings were given colored leg bands (numbered Fish and Wildlife Service bands dipped in airplane dope) designating their brood. This marking proved useful for observations of these birds in the late nesting and early post-nesting stages.

On-the-spot notes were made of activity observed at the colony with the time, and whenever possible specific birds and locations of each action recorded. At times it was found useful to prepare simple tables in which to record activity more quickly. In order to obtain accurate information on nest contents with a minimum of disturbance to the colony a specially designed periscope, dubbed a "Ripariascope," was made. This instrument lighted the nest chamber enabling one to view a nest and it contents quickly and without alteration of the burrow.

Spring Arrival

Bank Swallows usually arrive in the Madison area in the latter part of April. The arrival dates in the years 1947 through 1952 (according to the observations in the University of Wisconsin Zoology Department and Kumlien Club files) range from April 19th to 26th, the average date for the six years being April 22. Each of these observations was made by an experienced ornithologist, so it may be considered a positive record of presence of the species on that date. However, it is entirely possible that in some years the species may have been present for one or several days before the first observations recorded in this file. On the other hand such an observation may indicate the arrival of only a very few erratic individuals. Nevertheless, since these are the best available records of Bank Swallow arrival, it would seem worthwhile to consider their relation to climatological factors.

The April daily mean temperatures and dates of arrival for these years are shown in Figure 2 and summarized in Table 1. These data indicate that Bank Swallows will arrive in Madison earlier than the average date of April 22 when the mean temperatures of the preceding 15 days have averaged above normal. Arrival will be delayed beyond April 22 if the 15

Table 1

Arrival of Bank Swallows at Madison, Wisconsin

Year (In order of arrival dates)	Date of arrival	Mean Temperatures, °F			
		On date of arrival		Preceding 15 days	
		Temp.	Departure from normal	Temp.	Departure from normal
*1919	April 13	50	+ 6	44.1	+3.3
1948	April 19	69	+21	48.0	+4.5
1952	" 20	63	+15	44.1	+0.1
1949	" 22	58	+10	44.3	−0.7
1947	" 22	46	− 2	41.1	−3.8
1950	" 23	49	0	40.4	−4.8
1951	" 26	46	− 4	40.7	−6.0
Averages.....	April 22	55	+ 6.6	43.1	−1.8

*Not included in average.

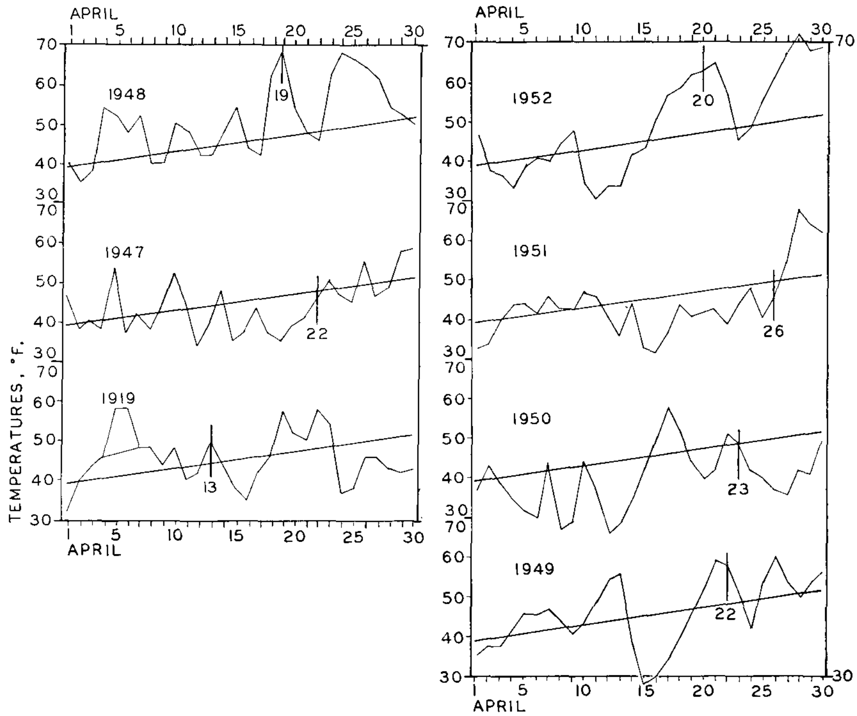

FIG. 2. Spring migration and temperature. Smooth diagonal line represents normal temperature; jagged line connects mean daily temperatures. Vertical bar indicates date of arrival of Bank Swallows at Madison.

days preceding arrival are considerably below normal for the period.

Taylor's observation (Schorger, 1931) of Bank Swallows on April 13, 1919, is the earliest known arrival date for Dane County. Since the temperature on that date was only six degrees above normal and the preceding 15 days averaged only 3.3 degrees above normal, it would seem that this was probably a record of a few birds advancing beyond the usual conditions for migration of the species, about a week ahead of the true migration front. Further evidence to this supposition is the fact that Taylor (unpublished field notes) did not find other late-arriving species of Hirundinidae unusually early in 1919.

Arrival of Bank Swallows at the breeding site may not be coincident with arrival in the area, particularly if the weather is cloudy and cold. In 1950 the species was observed at Madison on April 23. The next nine days were cloudy with mean temperatures below normal and, although there were additional reports of Bank Swallows in the area during this time, the birds were not seen in daily visits to the Nine Springs Creek site until May 3, when warm temperatures and clear skies again prevailed.

In 1951, on the other hand, the earliest arrivals were six birds seen at the Nine Springs Creek bank on the morning of April 26, a day of full sunlight. The following week was a succession of warm bright days, and an increasing number of birds was seen at the colony each day.

Nice (1937) found in her Song Sparrows that the timing of each of several activities, the taking up of territories by resident males, the spring arrival of migrants, and the start of egg-laying, was dependent on its own temperature threshold.

In unfavorable weather the early visits to the sand banks were brief and sporadic. Early arrivals were more likely to be seen foraging over bodies of water, which seem to be the best feeding grounds in April. On the first bright warm day the birds congregated at traditional breeding sites, entering old holes and clinging to any ledges or irregularities that lent support. Flights in large circles within 100 yards of the bank by individuals or small loose groups were frequent, but such flights lacked the close intense pursuit seen later in sexual chases. That interest in holes and ledges on the bank seemed to be by single individuals and that sexual chases were not observed suggest that few if any of these early visitors at the bank were paired.

Positive social forces are strong during these first appearances at the colony site. Usually all of the birds are engaged in the same activity. That is, all are circling overhead, or all are occupied on the bank. Alarm calls frequently put the entire group to flight.

Pair Formation

On successive favorable days the numbers of birds visiting the breeding site and the time they spend there increase. Gradually the increasing number of sexual flights and association of certain *pairs* of birds with particular burrows or areas of the bank suggest that more and more of these birds are paired.

Most Bank Swallows secure mates very quickly during early visits to the colony site. In other instances a week or more may elapse before a pair is formed. Observations of such cases reveal the following sequence of events in pair formation: An unpaired bird (a male in one instance where sex was subsequently determined) selects a burrow site. In the case of some early arrivals this may be a burrow of the previous year. Later the site is more commonly any suitable part of the bank on which the bird can maintain a foothold.

Having selected a site, or territory, a bird defends it against intrusion by use of vocal threats and physical force. Such vocal threat or "territorial song" is a loud coarse twittering, broken into long irregular phrases and directed with apparent vehemence with outstretched neck and bill pointed toward the intruder. These sputterings may be continued for a minute or more, and usually have the result of driving the intruder away. While territorial song seems to me to be aggressive in nature, certain observations suggest that it may serve to attract unmated birds. During this period when territories are being established, it is common to see groups of several or a dozen or more birds move along the bank in hovering flight, and again such birds will hover at a defended niche or even alight and cling to the bank. They are usually quickly driven off by the resident defenders, only to circle and return to the same or another defended ledge.

Against persistent intruders who perch very close, the defending bird intersperses his sputterings with forceful pushes with the bill. Still more forcibly a bird may fly from his ledge or burrow, turn, and, hovering over the intruder, grasp his neck feathers in his bill and thus pull him from the bank. Frequently two such birds become locked in combat and fall together from the bank, sometimes continuing their struggles for many seconds on the ground below.

One among those which continue to return to a defended spot is eventually tolerated and becomes recognized by the bird holding the territory as his mate. Sexual recognition probably depends on a female sexual characteristic of greater persistence in returning to a site in the face of apparent aggressive threat and attack.

One marked male defended his partially-completed burrow with great vigor following disappearance of his first mate. Later, having accepted a new mate, he was noticeably more tolerant of nearby birds whenever the mate was present in the burrow, than when she was away.

Birds entering burrows other than their own usually showed a certain hesitancy of manner contrasting with the deliberate actions of a bird entering its own burrow. Once a pair is formed both members of the pair share in territorial defense, both vocally and physically.

Maintenance of the Pairing Bond

Joint participation of paired birds in breeding activities, such as territorial defense and, as will be described later, burrow digging, nest building, incubation, and care of young, probably contributes to the strength of the attachment. Other activities which appear to serve more specifically toward maintenance of the pairing bond are sexual chase, mating song, and copulation.

Sexual chase is a prominent feature of the behavior of mated birds from the time of pair formation until incubation begins and it is continued (but much less frequently) into the incubation period. In sexual chase the female followed closely by her mate flies from the burrow and after either brief or extensive circling flight usually returns to the burrow. The male maintains close pursuit throughout whatever intricate maneuvers the female makes, and he sings continuously. I have observed sexual chase 10 or 15 times in marked pairs in which the sexes were known and found that in every case the female flew ahead of the male. In a few chases where the birds flew close enough, I noted, as Tooby (1947) frequently observed in the Sand Martin, that it is only the pursuer, that is, the male, that sings.

This song differs from territorial song and from mating song in its being given exclusively by the male. Further, it is neither as loud and harsh as territorial song nor as soft and murmuring as the mating song. During the burrow digging stage it was often noted that sexual chase occurred immediately upon the return of one member of the pair after a brief absence from the burrow. On two occasions a male sitting beside his mate near the burrow entrance was seen to nudge her gently in the side with his bill until she flew, seemingly upon his invitation. In each instance the male followed her in sexual chase.

While sexual chase is clearly an activity of mated birds, a pair will very commonly be joined by one or more additional birds. Unmated birds have been observed to leave their defended niches and join in the sexual chase of pairs from nearby burrows.

The *mating song* is such an inconspicuous form of courtship behavior that it is likely to pass unnoticed amid the more striking hubbub of territorial disputes and sexual chase. Its occurrence is probably more general than my two recorded observations would suggest, although it is mentioned in no previous studies of Bank Swallows.

The mating song is a very soft, pleasing twittering by both members of a pair simultaneously while sitting quietly side by side or facing each other in the burrow opening. It is much more subdued than territorial song or even that of the male in sexual chase, so that it can be heard for only a short distance. (My observations were from a blind 20 feet from the burrows.) It can not be heard at all if nearby birds are engaged in territorial song. Mating song is a continuous succession of notes, not broken into phrases like territorial song. In both cases observed the pairs were in the egg-laying phase and it may be an adjunct of copulatory behavior, commonly occurring as I believe copulation does, within the nest chamber.

Copulation

I have observed a number of apparently promiscuous copulations. At two different times dead Bank Swallows lying at the foot of the bank have been mounted repeatedly by several birds in quick succession in apparent attempted copulation, in one instance giving rise to an orgy of mountings both of the dead bird and of other copulating birds. A stuffed and mounted Bank Swallow skin placed on the ground likewise elicited many copulatory attempts, but no evidence of semen emission was found on the dummy.

On May 22, 1950, similar quick mountings were observed among a group of birds dusting on a dirt road 50 yards from the colony site at Nine Springs Creek. However, I have never observed copulation in a known or apparently mated pair of Bank Swallows and because of the absence of observations it seems likely that it takes place in the nesting chamber as Emlen (1954) described in the Cliff Swallow (*Petrochelidon pyrrhonota*).

Watson (1946) describes copulation of Sand Martins observed along a road in mid-June. Both the paired birds were crouched low and motionless with bills and heads touching the ground until the male, with his wings waving wildly and his body swaying from side to side, walked toward the female. He mounted her back and the female's wings were raised in a taut curve while coition took place. Then the female shook herself vigorously and both birds flew away. Watson's detailed description of this act implies a deliberateness not apparent in the copulations I have observed.

Burrow Excavation

Once pairing is accomplished the digging of the burrow or rehabilitation of an old burrow usually proceeds rapidly during favorable weather. The work is shared about equally by male and female. Unpaired birds may scratch briefly and intermittently in their defended niches, enlarging their footholds, but no bird without a mate was seen to dig more than a shallow hollow.

Rehabilitation of an old burrow sometimes consists of cleaning the burrow and removing old nesting materials from the nest chamber. In one case eggs left from the previous year were pushed out of the burrow along with newly-loosened dirt before the burrow was re-used. More frequently the burrow is dug deeper and a new chamber excavated. As the freshly-loosened sand is pushed out, the old nest and cavity become covered and partially filled.

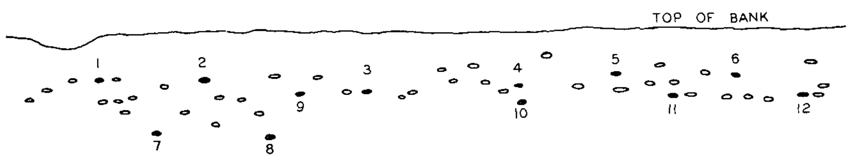

Fig. 3. Diagram of a portion of a Bank Swallow colony indicating by solid symbols burrows of which the rate of excavation is known. Burrows 1–6 are in locations above, and burrows 7–12 are in locations below others excavated at about the same time. Refer to Table 2 and Fig. 4.

TABLE 2
PROGRESS OF BURROW EXCAVATION

In burrows located in positions above others at same stage:

Date	Burrow Depth†					
	Nest 1	Nest 2	Nest 3	Nest 4	Nest 5	Nest 6
May 9		* 1				
10	5	8	8		* 1	
11	10	14	13		7½	
12	14	16	17		13	
13	18	17	20	* 3	18	* 3
14						
15	19	19 (7)	20	20	21 (6)	13
16						
17						
18	19	19	20	21 (6)	21	18 (6)
19	19	19	20	21	21	18

In burrows located in positions lower than others at same stage:

Date	Burrow Depth†					
	Nest 7	Nest 8	Nest 9	Nest 10	Nest 11	Nest 12
May 10	* 1	* 1	* 1	* ½	* 2½	* 1
11	1	1	1	1	3	1
12	2	1½	5	1½	9	1
13	2	2	11	2	16	3
14						
15	2	4	22 (6)	5½	21 (6)	15
16						
17						
18	16	11	22	19	21	21 (9)
19	19 (10)	16 (10)		21 (10)	21	21

*Digging started during preceding 24 hours.
†Underlined depth is earliest record of maximum depth in each burrow. Number in parentheses is number of days of digging to attain maximum depth.

If the chosen site is a smooth, newly-exposed surface and affords no projections on which to stand, the bird clings to any slight irregularity of the bank, with the tail and sometimes the wings spread to help support it while scratching with a side to side motion of the bill. The mate often takes a position close beside with an outstretched wing covering and helping to support the one digging. It sometimes appears that this supporting position results when the second bird lands so close to the first that it is unable to close the wing; nevertheless, it undoubtedly aids the bird occupied in digging to hold its position.

As soon as a narrow ledge has been scratched out, the birds support themselves on it in a horizontal position on one foot and frequently with the outer wing widespread against the bank below, while scratching out the beginning of the burrow with the upper foot. Both mates seem eager to take part in the digging, and they exchange positions at short intervals, the arriving bird often forcing his way inside and thus displacing the one at work.

The dirt is kicked back out of the opening with the feet. When the burrow becomes deeper, a shower of sand is sent back out of the burrow at each step of the entering birds, suggestive of a dog digging a deep hole. Contrary to popular opinion (Dawson, 1903; Forbush, 1929) dirt is not carried out in the mouth. I have frequently seen a Bank Swallow on leaving a burrow during the digging stage pick up a grain of sand in its bill and carry it away. This is commoner late in the nesting cycle and would seem to be a nest-cleaning activity.

As noted earlier, territorial defense, like digging, is shared by both members of the pair. The bird which is not engaged in digging is usually busy defending the site and frequently progress of excavation is interrupted when both members of a pair are involved in territorial defense. This is especially evident during the early stages of excavation.

When the burrow is very shallow, defensive threats are given while the swallows are clinging vertically to the bank, but as soon as the burrow is deep enough to accommodate both birds, the defender usually stands in the mouth of the burrow facing out. From this position the vocal threats and pushes are more effectively directed at intruders in positions below or to either side of the burrow, than toward those above the opening. Thus, in effect, higher positions become dominant to those below.

During the days when many pairs are starting their burrows, territorial threats and evictions occupy much of the time of the diggers, especially those occupying the more vulnerable low sites. Birds taking up sites in dominant positions above other territories are relatively free from chal-

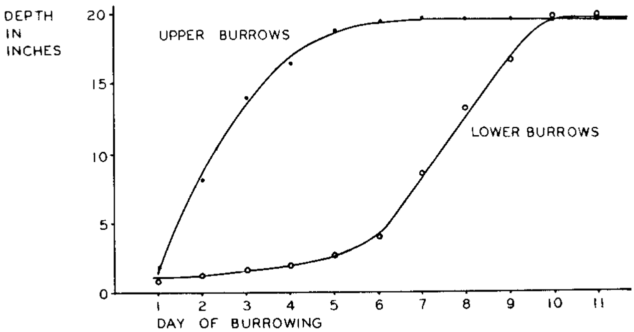

FIG. 4. Progress of burrow excavation. Dots represent mean depths of burrows 7–12 in Fig. 3 and Table 2.

FIG. 5. A Bank Swallow colony in a newly-excavated sand pit at Madison, Wisconsin. Burrows tend to be concentrated near the top of a high bank.

lenging attacks. As a result, burrows located high in relation to surrounding burrows increase rapidly in depth from the first foothold, while the excavation of low burrows is retarded for from two to five days until the hole becomes deep enough for one bird to dig undisturbed (Figs. 3 and 4; Table 2). Once a burrow is about three inches deep, excavation proceeds at a fairly uniform rate of about five inches a day irrespective of its position in the colony.

Thus, high positions would seem to be more favorable than low positions for establishing territories and digging burrows. This may explain why as is commonly observed, on a high bank offering a wide vertical extent of possible sites, the colony tends to be rather high and incidentally is safer from human and animal predators (Fig. 5).

The distance between adjacent burrow openings is determined by the area which a pair can successfully defend. In Table 3 are shown distances between burrow openings (measured center to center) in a densely concentrated colony where the soil was essentially uniform through a vertical extent of eight feet. This colony (Fig. 6) was in a new site and all the burrows were dug in 1952. Minimum spacing of openings was four inches, a majority being from five to seven inches apart. Territory in Bank Swallows is functional in minimizing the chance that adjacent burrows will run together or that the walls between them will break. In every case I have found (14 records) where two or more burrows met, only one has been completed and used for nesting. Stoner (1936) records instances of two nests located side by side in a common nest chamber after the thin

TABLE 3
MINIMUM DISTANCES BETWEEN BANK SWALLOW BURROWS

Distance to nearest burrow in inches	Frequency			
	From HIGH burrows	From MIDDLE burrows	From LOW burrows	Totals
4	2			2
5	10		7	17
6	6	3	2	11
7	13	5	2	20
8	2	3	3	8
9		2	2	4
10		1	2	3
11	1		1	2
12	1		3	4
..				
17			1	1
Total frequencies...	35	14	23	72
Mean distances....	6.4	7.5	8.1	7.3

partition between had broken down, but it is not stated at what stage the walls broke or whether either of such nests was deserted.

Positive social forces in a colony tend to keep the burrows concentrated. In locations providing extensive vertical banks that appear suitable for nesting, it is frequently found that one particular section is utilized by all or a vast majority of the birds. Adjacent sites having similar physical characteristics may remain untenanted. In several instances small groups of birds established territories at such nearby locations after nesting at the

FIG. 6. Typical burrow spacing at a new site having a wide vertical extent of essentially uniform soil.

main site was well under way. Thus, at Nine Springs Creek in 1951 the traditional site near the road attracted the earliest birds of the colony. Next a small group of about 68 birds took up sites 350 yards upstream where only a couple of pairs nested in 1950. The latest nests were found in four smaller groups between these, where there had been no nesting in previous years. The spatial relationships of these sub-colonies with the number of nests and mean hatching dates in each are shown on the map of the colony (Fig. 7). Stoner (1941) has found by banding studies that the majority of breeding members of a colony reassemble in the same colony season after season.

It has been stated (Stoner, 1936; Bent, 1942) that burrows excavated in loose sandy soil tend to be deeper than those located in gravelly or clay banks. Although the banks used as colony sites in Dane County were fairly uniform in soil texture, a test of this correlation was made at 10 sites in eight colonies in Dane County. Samples were taken and analyzed for soil texture by the hydrometer method (Taylor, 1948). The results of these 10 analyses together with mean burrow depth in each location are shown in Table 4. Soil types varied from *sand* (94 per cent sand) to *sandy loam* (65 per cent sand, 35 per cent silt and clay). The percentages shown for soil textures are only roughly indicative of the degree of compactness, which is partially dependent on other factors. Nevertheless, a positive correlation was found between the mean burrow depths at each site, ranging from 20.4 to 36.2 inches, and per cent of sand in the soil. (The deep burrows at the Sprague-Dawley pit were a marked exception). At each of the colonies where

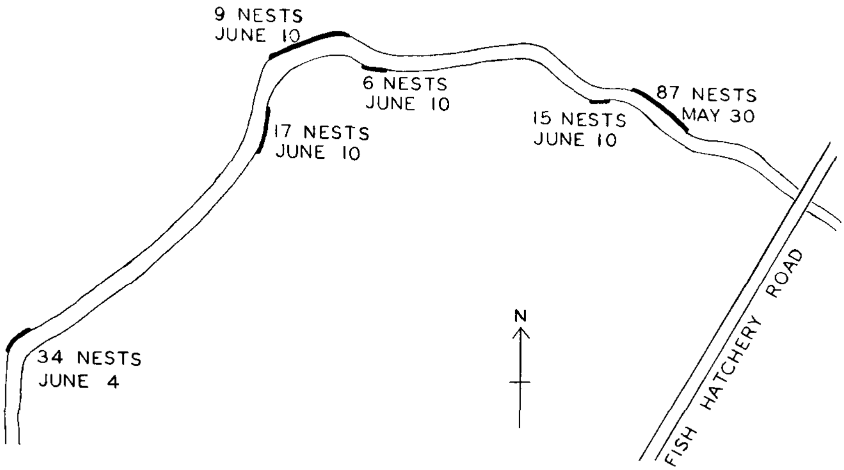

Fig. 7. Nine Springs Creek Colony. The number of nests and mean date of hatching in 1951 are given for each sub-colony.

TABLE 4
SOIL TEXTURE AND BURROW DEPTH

Colony	Mean burrow depth (inches)	Soil Texture		
		per cent sand	per cent fine material	Class
Wisconsin River, Area 1	36.2	92	8	Sand
Wisconsin River, Area 2	33.0	94	6	Sand
Columbia Co. V, Road cut	28.5	93	7	Coarse sand
Black Earth Creek, sandy layer	25.6	94	6	Coarse sand
Black Earth Creek, loamy layer	22.2	85	15	Loamy sand
Dane Co. Hwy. Q, Sand pit	21.6	85	15	Loamy sand
Monona Road cut, lower layer	24.2	83	17	Loamy sand
Monona Road cut, upper layer	20.4	80	20	Loamy sand
Nine Springs Creek	20.7	75	25	Sandy loam
Sprague-Dawley pit	26.5	65	35	Sandy loam

two distinct soil layers were used by the swallows (Black Earth Creek and Monona Road cut), burrows were deeper in the more sandy layer. As observed at these and other colonies where stratification occurs, a preference was shown for the more sandy layers and gravelly layers were avoided (Figs. 8 and 9).

Excavation of the nest chamber requires several days after the burrow has reached its maximum depth. The floor of the chamber is about two inches below the level of the burrow so that the completed nest and eggs are below burrow level. This was convenient for my observation with the Riparia-scope, since the eggs or newly hatched young were always well below the instrument where they could be clearly seen and not disturbed or damaged.

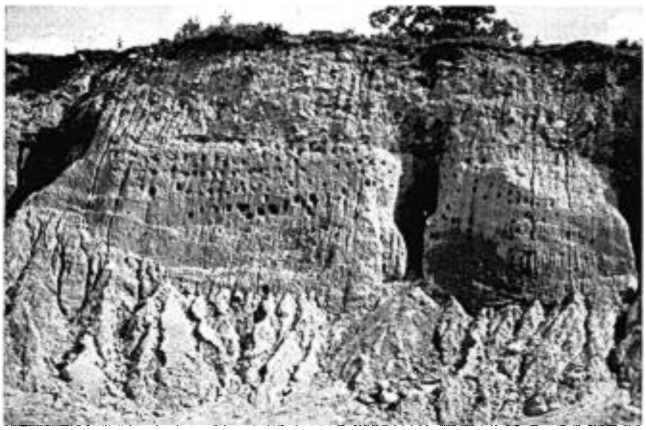

FIG. 8. Burrows in horizontal rows are excavated in thin layers of coarse sand in this old sand-pit, Racine County, Wisconsin.

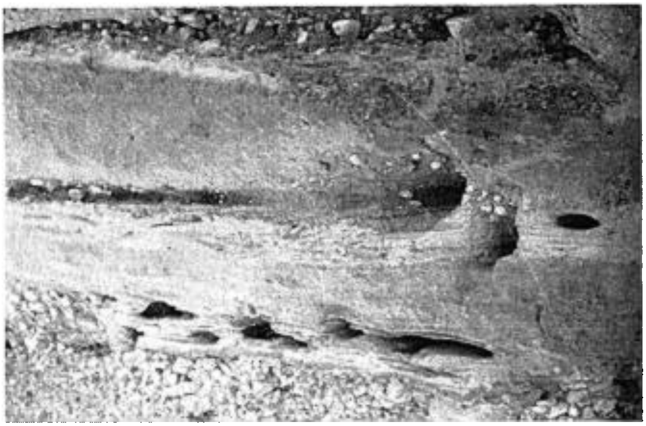

FIG. 9. Bank Swallow excavations in coarse sand layers. Gravelly layers are avoided.

NEST BUILDING

Nest building begins as soon as the nest cavity has been excavated and both members of a pair contribute to its construction. Rather than "nest *building*" it might be more accurate to say "accumulation of nesting materials," for the nest is a somewhat formless mat of whatever materials are most readily obtainable. Fine grass blades and stems are the most common materials in most of the colonies where I have collected. Roots are torn from the eroding bank for use in nests, but the birds seem to prefer to use materials that can be picked up easily. Near farmyards straw is commonly used. The birds are quick to make use of any such materials dropped by others at the foot of the bank. At Nine Springs Creek I have watched Bank Swallows make repeated trips for dried grass from a roadway about 100 yards from the burrows.

The mat is about an inch thick in the middle and thinner toward the edges, conforming to the saucer-form of the chamber floor. When the eggs are laid it is loose and flat-topped. As incubation proceeds the center becomes depressed into a shallow hollow. A lining of feathers is added to the nest during incubation. Feathers, like grass, are brought to the nest by both members of the pair. As the lining is added the eggs are, of course, kept on top of the feathers.

Of thirty nests where the condition of feathering was noted and the stage of egg-laying or incubation known, only one contained a feather before egg-laying was completed and three nests still had no feathers after five and six days of incubation. Usually the first feathers are brought in on the second or third day of incubation and the nest is well lined with feathers

TABLE 5
CLUTCH SIZE IN THE BANK SWALLOW

Size of Clutch	Frequency		
	Before June 15	After June 15	Totals
2	–	2	2
3	3	1	4
4	14	13	27
5	64	5	69
6	23	–	23
Totals..................	104	21	125
Mean clutch size.........	5.0	4.0	4.8

before the eggs hatch. In a few instances I have seen feathers brought to the nest after the nestlings are a week old.

With few exceptions white chicken feathers were used, but colored feathers have also been noted. The number of feathers brought to the nests is much greater in colonies adjacent to chicken yards.

Stealing of feathers from nests left unattended was a common practice at the Nine Springs Creek colony.

EGG-LAYING

Observations with the Ripariascope indicate that eggs are laid at the rate of one per day until the clutch is complete. Data on clutch size obtained in this study are summarized in Table 5 and compared with reports from the literature in Table 6. In 125 completed clutches, I found the usual number of eggs to be five, although clutches of four and six eggs are not uncommon and a small number of clutches of two and three eggs were found being incubated.

I have no records of second nestings in this locality. Clutches started after June 15 were known to be or could be attributed to re-nestings of birds whose first nest was destroyed, usually by slumping of the bank. In one colony under daily observation, marked individuals in a re-nesting attempt took over a burrow recently left vacant by the brood of another pair. In some cases where re-nesting birds utilized old burrows, these were cleaned or dug deeper and a new nest built. In at least one instance a new clutch of eggs was laid in a dirty nest from which a brood recently fledged and to which no new nesting material had been added. The latest date I have found for the starting of a clutch was July 5, 1950. Mean size of clutches laid after June 15, and believed to be re-nesting attempts, was 4.0 eggs as compared with 5.0 eggs in first clutches (Table 5).

Stoner (1936) states that very few birds (his figures suggest about four per cent) rear second broods. His assertion that the second broods are raised is based on one or more observations of a second clutch of eggs in a burrow from which young were fledged earlier in the same season. In the light of my observations this interpretation appears unwarranted. Unfortunately Stoner's statements were misconstrued when Gross (Bent, 1942) says that Stoner "presents concrete evidence that two broods are the usual thing in the colonies studied intensively by him."

Wilson (1812) makes the general statement that the Bank Swallow commonly has two broods. Audubon (1840) says that this species "generally rears two, and sometimes three broods in a season" in Louisiana, produces two broods in Kentucky, and "lays only once" in Newfoundland and Labrador. I was able to find no recent observations to confirm these statements. Oberholser (1938) states that there is "no definite nesting record for Louisiana."

Incubation

That incubation usually begins before the clutch is complete is evident from the variation of stages of development found within single clutches of eggs or broods of nestlings. Nearly every clutch, even those just completed showed a difference in apparent age of two to three days between the embryos of greatest and least development. In about two out of 31 instances the four or five embryos in one nest were at the same stage (day) of

Table 6
Reported Clutch Size in *Riparia riparia*

Authority	Locality	Clutch Size
Lack, D. (1947)	England	4–5
" "	Central Europe (Saxony)	5 (6)
" "	Eastern Galicia	5–6
" "	Norway	(4) 5 (6)
Forbush (1929)	New England States	3–7
Jourdain (in Witherby, *et al.*, 1940)	Great Britain	Usually 4–5 Sometimes 3, 6, or 7
Niethammer (1937)	Germany	5 (4–7)
Stoner (1936)	New York State	Early broods: 4 or 5 Late broods: 3 or 4
" "	Iowa	5 or 6 eggs (4 or 5 young)
Cory (1909)	Illinois and Wisconsin	3–6
Petersen (this study)	Dane County, Wis.	Before June 15: 5.0 After June 15: 4.0 Entire season: 4.8

TABLE 7
PRESENCE OF SEXES IN BURROWS AT NIGHT

Stage	Frequency*				Both sexes present	
	Total	Female alone	Male alone	Both sexes present	Female off first	Male off first
Nest-Building	4	1 (25)	1 (25)	2 (50)	2	0
Egg-laying	4	2 (50)	1 (25)	1 (25)	?	?
Incubation	32	21 (65.6)	2 (6.2)	9 (28.1)	3	6
Parental	36	23 (63.9)	6 (16.6)	7 (19.4)	4	3
Totals	76	47 (61.8)	10 (13.2)	19 (25)	9	9

*Actual number followed by percentage of total (in parentheses).

development and so had apparently been incubated an equal length of time. The extent of difference between oldest and youngest embryos in each clutch is not related to clutch size. It is evident therefore that incubation begins with the laying of the third, fourth, or fifth egg. Or it may be as Purchon (1948) found in the Swallow (*Hirundo r. rustica*) that incubation occurs for a short time each day from the laying of the first egg, and is increased each day until the maximum is reached. (In the case cited, incubation determined by day-long observations throughout the incubation period began with 10 per cent daytime incubation on the day the first egg was laid and increased to a maximum of 70 per cent daytime incubation on the eighth day.)

In two instances Stoner (1936) verified by dissection his observation that males were sitting on the eggs during daylight. By observation of marked birds I have found that the members of each pair share time on the eggs about equally during the daylight hours.

In Bank Swallows, as in most other passerines, only females develop an incubation patch. Ryves (1943) and Bailey (1952) believe an incubation patch is necessary for true incubation to occur and so consider that even in species in which males regularly take turns on the nest as in the Bank Swallow, males are incapable of true incubation. Bailey believes that in passerines the female alone will be found sitting on the eggs at night. My collecting records show (Table 7) that in 32 burrows from which I collected Bank Swallows during the incubation stage, the female was alone on the nest in 21 cases (65.6 per cent), both sexes were present in nine burrows (28.1 per cent) and in two instances (6.2 per cent) only the male of the pair was present in the burrow. In the nine instances where both sexes were present, the male left the nest before the female six times, and the female came off the nest first three times. It cannot be assumed however, that the incubating member of a pair will sit more assiduously.

Whether male Bank Swallows or any male passerines actually incubate, that is, raise the temperature of the eggs sufficiently to permit development of the embryos, can be positively determined only by studies of the egg temperatures produced by the males and the temperatures required for development.

In July, 1952, I placed the outdoor bulb of an Airguide indoor-outdoor thermometer among the eggs in a nest where the parent birds were color-marked for individual recognition. Access to the nest chamber was obtained by a hole dug behind the burrow. The thermometer scale was situated above the bank in such a manner that temperature readings could be made with binoculars from a blind while each entrance and exit at the burrow mouth could be observed.

In the first trial both birds deserted the nest. The second attempt was unsuccessful because the thermometer bulb was inadvertently pushed out of the nest. Results obtained in a third nest are shown in Figure 10. The female returned to the nest just once during the observation period and flew out with a feather almost immediately. During the next two and one half hours the male of the pair entered the burrow seven times for periods of two to 19 minutes, each time producing a sudden rapid increase in the nest temperature by as much as 21° F. above that of the unincubated nest. During the longer periods of 19, 17, and 18 minutes on the nest, temperatures of 94, 94, and 96 degrees F., respectively, were attained. Due to the size of the thermometer bulb (9 mm. diameter × 50 mm. in length) it was undoubtedly not covered as efficiently as a clutch of eggs alone would be. In normal incubation there is direct changeover between the members of a pair at the nest, so that eggs would not be subjected to periods of cooling between spells of incubation. It remains for further experiments of this type to provide temperature data of eggs incubated alternately by male and

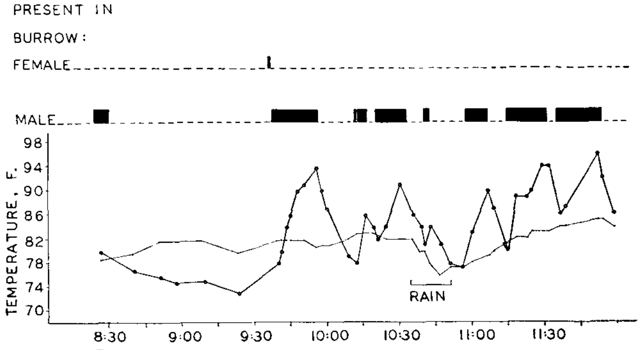

Fig. 10. Temperature of nest incubated by male Bank Swallow, July, 1952. Air (thin line) and nest temperatures were read from an Airguide indoor-outdoor thermometer.

TABLE 8
INCUBATION PERIOD IN THE BANK SWALLOW*

Clutch size	Total frequency	Class frequency		
		13 Days	14 Days	15 Days
3	1	–	–	1
4	2	–	1	1
5	2	–	2	–
6	6	3	1	2
Totals..........	11	3	4	4

*Days from laying of last egg to first egg hatching.

female. Nevertheless, the data presented here are positive evidence of male incubation.

The incubation period.—Incubation, from the laying of the last egg to the hatching of the last egg (when all eggs hatch), was determined in only two nests. It was found to be 15 days in both. In all nests the incubation period, counting from the laying of the last egg to first hatching, was from 13 to 15 days, as shown in Table 8. Evidence presented above indicates that incubation usually begins one or two days before the last egg is laid. Therefore it seems probable that the *actual* incubation period under natural conditions is 15 days, and apparent periods of 13 or 14 days occur when incubation begins two or one days, respectively, earlier than completion of the clutch.

Incubation periods recorded in the literature (Table 9) range from 12 to 16 days.

PARENTAL BEHAVIOR

Since incubation usually began one or two days before the laying of the last egg, hatching of a brood occurred over a period of two or three days and the young in each brood showed a difference of two or three days

TABLE 9
REPORTED INCUBATION PERIODS IN *Riparia riparia*

Authority	Incubation period
Evans (in Bergtold, 1917)	12 or 13 days
Burns, 1921	12 – 13 days
Stoner, 1936	14 – 16 days
Jourdain (in Witherby, *et al.*, 1940)	14 (12 – 16)
Niethammer, 1937	12 – 16
Baerg, 1931	13 – 14
Petersen (this study)	Apparent: 13 – 15 Actual: 15

in development. Egg shells were carried from the nest soon after hatching occurred. Three aspects of parental behavior are considered here: brooding, nest sanitation, and feeding.

Brooding.—The nestlings were brooded almost constantly on the day of hatching, the parents alternating on the nest. On successive days the amount of brooding decreased by a shortening of the length of each period on the nest. Six successive periods of brooding on one nest on the day of hatching were from seven to 28 minutes duration (28, **11**, 7, **10**, 7, **11**, periods by female in boldface). Two days later the same number of periods of brooding was observed per hour, but each period was only from three to five minutes long and longer periods of absence from the nest intervened. My observations do not substantiate Beyer's statement (1938) that the female does almost all of the brooding. His statement is based on his belief that he could distinguish between the sexes by the manner of movement of the birds. My birds were color-marked and the sexes known.

I have no observations on daytime brooding periods after the third day, but Beyer observed that by the seventh day brooding had practically stopped and the parent birds only occasionally sat on the young, usually for less than one minute at a time.

Until they are 10 days of age, the nestlings may be brooded by either or both parents at night. I collected the parent birds at night from 36 burrows containing nestlings (Table 7). The female was found alone on 23 nests, the male alone on six, and both male and female parents were present on seven nests. Observations of more than 100 nests at this stage indicates that the parents rarely spent the night in the nest after the young were 12 days old.

Nest Sanitation.—My observations agree with Beyer's finding that during the first days after hatching, the excrement of the nestling was swallowed. I have seen fecal sacs carried from the burrows when the nestlings were four days old. In the nest watched by Beyer all the excrement was carried away when the nestlings were seven days old and at nine days the young left the nest chamber to void in the burrows. I have observed that by 14 days they run almost to the burrow entrance and turn around to void. Bank Swallow nestlings never eject fecal sacs out of the burrow, so the ground below a colony does not become fouled with excrement as does the area below a Cliff Swallow colony.

Both parents assisted in nest sanitation. If excrement were present it was nearly always removed by the next bird leaving the burrow. Usually only one fecal sac was carried away at a time. If more than one was present, the bird did not return immediately for the second, but it was carried out after the next feeding.

There was a definite tendency for the parent birds to pick up *something* as they left the burrow. If no droppings were present, the birds would pick at or pick up a grain of sand or a tiny pebble as they ran out of the burrow.

Excrement is removed less promptly in the later stages of nestling life. Beyer reported that nest sanitation had stopped when the young were 17 days of age, but his observations continued for only an hour on that day. I have found that while the droppings may be left in the burrow for a time after 17 or 18 days, nest sanitation is usually resumed at irregular intervals until the young leave the burrow. In one instance a marked female returned to her own burrow and removed excrement left by her nestlings when they roosted there at 28 days of age.

Feeding.—My observations of feeding of Bank Swallow nestlings include data on six pairs of marked birds of known sex feeding broods in which the number and hatching date of the nestlings was known.

The mean feeding rate found in 33 nest-hours of observation (morning and mid-afternoon hours on fair, warm days) was 24.7 feedings hourly per nest. Marked differences are found in a comparison of feeding rates reported for this species from other localities during apparently similar weather (Table 10A). These differences are difficult to explain without more extensive study of feeding rates under varied conditions.

TABLE 10

NESTLING FEEDING RATES

A. Mean Hourly Feeding Rates.

Source of data	Locality	Hours of observation	Feeding rate
Petersen, this study	Wisconsin	33	24.7
Beyer, 1938	Ohio	2	24
Moreau and Moreau, 1939	England	24	33.3
Stoner and Stoner, 1941	New York	56	17.1

B. Feeding Rate and Brood Size.

Brood Size		Moreau	This study	Total
	Hours observed	14	21	35
3	Rate/nest	32.4	24.1	27.4
	Rate/nestling	10.8	8.0	9.1
	Hours observed	10	12	22
4	Rate/nest	34.7	25.7	29.8
	Rate/nestling	8.7	6.4	7.4

C. Feeding Rate of Sexes.

Number of pairs	Hours of observation	Feeding rate by male	Feeding rate by female	Total mean feeding rate
6	27	14.8	9.7	24.5

TABLE 11
FEEDING RATE AND NESTING AGE

This study			*Previous studies*			
Age	Hours observed	Feeding rate*	Age of nestlings	Hours observed	Feeding rate*	Reference
			3	2	24	Beyer, 1938
			2–4	14	14.1	Stoner, 1941
8	1	25	5–9	35	19.3	" "
9	2	19				
10	0	–				
11	3	20.7	10–12	7	18.3	" "
12	7	25.8				
13	14	30.5	13	2	28	Moreau and Moreau, 1939
14	3	24.7	14	2	44	" " " "
15	2	26				
16	1	24				
17	3	21				
18	7	22.4	"Nearly ready to fly"	20	32.8	" " " "
19	1	19				
20	2	20.5				

*Mean hourly feeding rate per brood.

My observations were spread over a number of days when the nestlings were from 8 to 20 days of age. The rates found for each day of nestling age (Table 11) indicate no trend during this span of nestling life. Data from other studies are presented in a parallel column, but since nestling age is not known exactly in all cases and conditions of time and locality are not uniform, detailed comparisons are not warranted.

The feeding rate at each nest was not proportionately greater in larger broods. Thus, the number of feedings per nestling was greater in smaller broods (Table 10B). In 35 hours of feeding broods of three nestlings (including data from Moreau and Moreau, 1939) the mean rates per hour were 27.4 feeding per nest or 9.1 feedings per nestling. Broods of four nestlings, observed for 22 hours were fed 29.8 times per hour, a mean of 7.4 feedings per nestling. The same relationship between feeding rate and brood size was found in Cliff Swallows (Petersen, MS), in the European Robin, *Erithacus rubecula*, (Lack and Silva, 1949), and Swift, *Apus apus*, (Lack and Lack, 1951).

Twenty-seven hours of observations of the six pairs in which the sex of each individual was known indicate that, as Beyer believed, males feed the nestlings more frequently than do females (Table 10C). The mean hourly feeding rate by males was 14.8, and that for females, 9.7, a total mean feeding rate of 24.5. Individual variation was noted, however, and it cannot be assumed that the bird feeding more frequently in any pair is the male.

Beyer noted during early days of nestling life as I found in older birds, that only one nestling was fed in each visit of the parents. A food call given by the adult bird as it enters the burrow is described by Beyer as a "series of particularly sweet fine notes higher in pitch than the usual Bank Swallow call." The nestlings were first heard to give a similar call at four days of age. I have found that nestlings will give this call whenever the burrow is partially darkened as though by an entering bird.

At nine days the nestlings rush toward the parent in the burrow to be fed. By 12 days of age the nestlings wait about six inches from the burrow entrance to be fed. During the last several days in the nest the fledglings are fed much of the time at the burrow entrance. Two to four or five birds sometimes jostle for front position in the burrow while waiting to be fed. When the parent approaches, each of the fledglings gives a series of loud sharp chirps, repeating it incessantly until he is fed, or until the adult bird leaves. After a young bird has been fed, he usually backs out of sight behind his mates or turns around and enters deeper into the burrow, giving up the front position to one of those who remain.

Eleven broods of nestling Bank Swallows were given color bands designating their home burrows. Eight of the female parents of these broods were individually marked. Observations of these birds indicate that young Bank Swallows fly from the burrows at about 20 days of age, but return to some burrow, frequently their own, during part of the day and for night roosting for several days. Nestlings as old as 28 days have been seen roosting in their own burrows.

The following observation suggests that the first flight of fledgling Bank Swallows may be brought about by a reduced feeding rate and by vocal urging of the parent birds. A marked adult male hovered in front of his own burrow where his three fledglings, 23 days old, were at the entrance calling and gaping. Presently he alighted at a neighboring hole a foot away, alternating his lower-pitched single note with the calls of the young birds. After perching less than a minute he flew back and forth in an area about 10 yards in diameter near the burrow entrance, continuing his low-pitched *buzz*, seemingly in answer to the continued begging of the young. Again he landed at a nearby burrow. This performance was repeated about 12 times in half an hour. Then one of the nestlings flew from the burrow in response to the alarm note of a bird flying overhead. During this period of observation, no food was brought to the nest, but three days later both parents were seen feeding one of the young that remained in or had returned to the burrow. Luring of the young from the nest by irregular or feint feeding or by calling has been reported by Nice (1943) in a number of altricial species, including Barn (*Hirundo rustica*) and Tree (*Iridoprocne bicolor*) swallows.

Stoner (1942) found young Bank Swallows returning to their own or other burrows after their initial flights. My observations of feeding of marked fledglings (from 20 to 28 days old) by marked adults indicate that adult Bank Swallows recognize and will feed their own young which have returned either to their own or to other burrows. None of the marked adult birds was seen feeding a juvenile other than its own, even in the home burrow of the adult. Juveniles landing in a burrow not their own were in several instances attacked or pushed out by the adult resident. Nice (1943) notes that birds with altricial young do not recognize their eggs or nestlings, but that her Song Sparrows learned to recognize their young individually before independence was attained.

Post-nesting Behavior

At the Bank Swallow colonies I have observed, loafing sites such as nearby wires were used very little during the breeding season. At the time when young birds are leaving the nest, however, nearby wires are occupied for longer periods each day, and by increasing numbers of birds, both adult and immature.

During the first two weeks in August, 1950, small bands of recently-fledged young birds were seen on several occasions at the Nine Springs Creek colony engaged in entering holes, scratching at the bank and toying with nesting materials. On August 14 when several broods were still being fed in the burrows about 800 Bank Swallows, including a large proportion of juveniles, visited the colony. About 100 of these birds perched on wires near the bank, while others were engaged in cleaning and enlarging burrows or digging new holes. A constant twittering was heard from the birds. Such behavior suggests abortive nesting behavior.

During August, 1951, a group of post-nesting adults and juveniles was seen near a breeding site a mile west of Mazomanie. The birds sunned and dusted themselves on a long earth bank with a slope of about 30 degrees. Close observation showed that many of the birds were digging shallow holes, none exceeding five inches in depth. It is interesting that a slope unsuited as a breeding site should nevertheless be used for this post-nesting burrowing activity. Stoner (1936) observed post-season burrow-digging by juveniles at some of his colonies in New York State.

In a migrating flock of 2,000 Bank Swallows seen on September 13, 1945, Thom (1947) observed frequent attempted copulation and "threat displays." I saw similar attempted copulations among swallows in a small flock on a road in late July, 1952. I could not detect whether any of the individuals taking part in this activity were juveniles.

The annual appearance of huge flocks of Bank Swallows at traditional roosting sites has been described for a number of localities. Abby F. C. Bates (1895) described the activities at such a roost near Waterville, Maine. O. Widman (1907) states that such flocks begin to accumulate in the Mississippi River bottoms at St. Louis, Missouri, as early as July 1 and that migration continues throughout the month of August, all the birds having left by mid-September. Flocks of Bank, Tree, and Barn Swallows have been described by E. J. Sawyer (1918) in Jefferson County, New York. The largest Bank Swallow flock recorded was one near Toledo, Ohio, in 1931, estimated by Louis Campbell (1932) to include 250,000 birds.

The largest concentration of Bank Swallows I have observed was the flock of 800 that visited the Nine Springs Creek colony site in August, 1950. A group of about 700 birds spent several days in July, 1950, on the Mendota State Hospital farm near the north tip of Lake Mendota. Most of the birds perched along the wires or in large willow trees near the road, but several hundred sunned themselves on the bituminous-surfaced road. This location annually attracts such post-breeding flocks.

In the years 1950 through 1952 all the Bank Swallows had migrated from the Madison region by September 1. Schorger (1931) states that while Bank Swallows usually have migrated from the Madison area by September 1, some individuals may remain into September. The latest date for the species in his records is September 11.

II. Physiological and Morphological Cycles

Procedures for Collection and Autopsy of Specimens

For the study of the physiological and morphological cycles, adult Bank Swallows were collected from their burrows at night throughout the breeding season. A total of 114 adults (79 females and 35 males) was collected during the two years, 1950 and 1951. These were representative of all stages of the behavior cycle from burrowing to late parental stages (Table 12).

Table 12
Numbers of Specimens Collected

Phase of Cycle	Females	Males	Totals
Burrowing	2	0	2
Nest-building	11	8	19
Egg-laying	7	4	11
Incubation	28	10	38
Parental	31	13	44
Totals	79	35	114

After the birds had retired to their burrows for the night and darkness had fallen a number of burrows sufficient to provide the specimens needed were plugged with paper, so that our activities at the bank would not put these birds to flight. Then one burrow at a time was opened and the birds attracted to a flashlight at the entrance where they were captured by hand. Each specimen or pair of specimens was autopsied immediately before another was taken. It was found that specimens could be handled most advantageously by two people working together, one at the bank obtaining the birds and nest contents, and the other doing the autopsy in a laboratory set up in the back of a panel truck. The procedure used for each bird was as follows:

1. The adult bird was taken from the burrow and handed to the laboratory man for autopsy. Meanwhile the bank man measured the burrow, noted the condition of the nest, and collected the eggs and young, which were preserved in 10 per cent formalin for later examination.

2. The specimen was killed as quickly as possible by decapitation and the blood which flowed from the carotid vessels collected into a centrifuge tube.

3. A 0.02 ml. sample of blood was pipetted into 5 ml. of dilute tungstic acid in another centrifuge tube for later glucose determination. The pipette was rinsed with the dilute tungstic acid, then the tubes were corked and the pipette prepared for the next sample by rinsing successively in water, ethyl alcohol, and ether.

4. The bird was weighed on a triple beam balance.

5. The brood patch or ventral apterium was removed by dissection and preserved in Mossman's FAA fixative.

6. The body cavity was opened and the lower back region containing the testes or ovary and oviduct, was removed and preserved in FAA fixative.

The blood samples for glucose determination were refrigerated until the test was run the following morning. The whole-blood sample was frozen for later determination of serum calcium. The preserved organs were held for subsequent measurement and examination.

Determination of Reproductive Stages

The *phase* of reproduction of each specimen was readily noted by examination of the burrow or its contents. Thus, the following phases are represented by specimens: (1) burrowing, (2) nest building, (3) egg laying, (4) incubation, and (5) parental phase. Within each phase criteria were established as described below for determining the more precise reproductive *stage.*

Burrowing.—Only two specimens were secured before the start of nest building and these were from a late stage of burrowing.

TABLE 13
NEST BUILDING STAGES

Stage (Day)	As Determined by Ovary Condition:	As Determined by Nest Condition:
1	No ova over 2 mm. in diameter.	Few bits of nesting material.
2	Largest ovum 2 to 5 mm. in diameter.	Small amount of nesting material.
3	Largest ovum 5 to 8 mm. in diameter.	Moderate amount of nesting material.
4	Largest ovum over 8 mm. in diameter. No ova in oviduct.	Large amount of nesting material.
5	First ovum in oviduct.	Nest apparently complete.

Nest building.—Five stages of nest building were designated (Table 13). In female specimens, the development of the ovary took precedence over condition of the nest in determining the stage since the ovary more accurately indicates time before start of the egg-laying phase. Males collected with their mates were placed in the stage determined by the ovary condition of the female. Reproductive stages of males collected alone during this phase were determined solely by condition of the nest. Nest building does not proceed at a uniform rate in all pairs. Consequently the intervals between stages of nest building are not strictly uniform, although stages 2, 3, 4, and 5 as determined by ovary development do correspond approximately to days.

Egg laying.—Stages of egg-laying correspond to the number of eggs laid, except that where examination of ovary and oviduct indicated that a clutch was complete with less than five eggs (the most frequent number) it was placed in stage 5 of egg laying.

Incubation.—Stages of incubation of collected adult specimens were determined by the stage of development of the embryos measured in days, based on a series of embryos taken after known periods of natural incubation (Petersen, MS). Complications were presented by the fact that embryos in any one nest usually showed a range of development equivalent to two or three days of incubation. Adult specimens were assigned arbitrarily to the stage represented by the youngest or least-developed embryo.

Parental phase.—During the parental phase the specific stage to which each specimen was assigned is equivalent to the determined age of its youngest nestling. In order to establish criteria for aging nestling Bank Swallows observations and measurements were made of nestlings of known age.

The most apparent physical changes in young Bank Swallows during the nestling period are changes in weight and the development of plumage (Fig. 11).

The daily increase in weight for the first 11 days is so great that an average daily weight curve is useful in aging nestlings during this period. After the twelfth day the daily increment decreases until a maximum weight is attained on the fifteenth to seventeenth days, followed by a steady loss of weight to the day of fledging.

The most marked and easily observed feature of feather development is that of the ninth primary, which breaks through the skin on the seventh or eighth day and reaches a length of over 60 mm. at the time of fledging. The daily increment is so great that the length of the ninth primary becomes a useful aging criterion.

The ranges in weights on consecutive days overlap even during the first 12 days of development; likewise, the ranges of lengths of the ninth primary feathers on consecutive days overlap throughout their development. Consequently the age of nestling Bank Swallows as determined by these criteria is approximate and may be in error by one day in either direction.

Body Weight

The body weights of 121 Bank Swallows were obtained at autopsy throughout the breeding cycle. The mean weight of 82 females (Fig. 12) was 14.8 grams (range 11.4-18.5). Marked fluctuations were found during the cycle: (1) A rapid increase during late nest-building stages, paralleling the development of the ovary and oviduct, brought body weight to a maximum of 17.5 grams (mean weight of three individuals) on the day preceding laying of the first egg. This was an increase of 2.7 grams (18.2 per cent) above

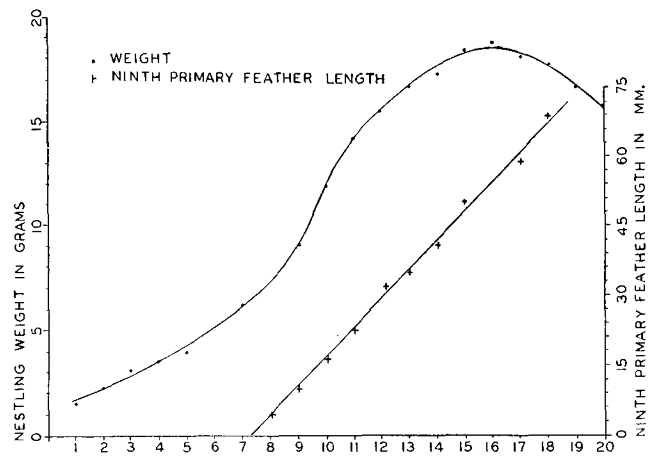

Fig. 11. Body weight and length of ninth primary feather in nestling Bank Swallows. During the first 11 days of nestling life, body weight was used as an aging criterion. Length of ninth primary feathers was used as an aging criterion for older nestlings.

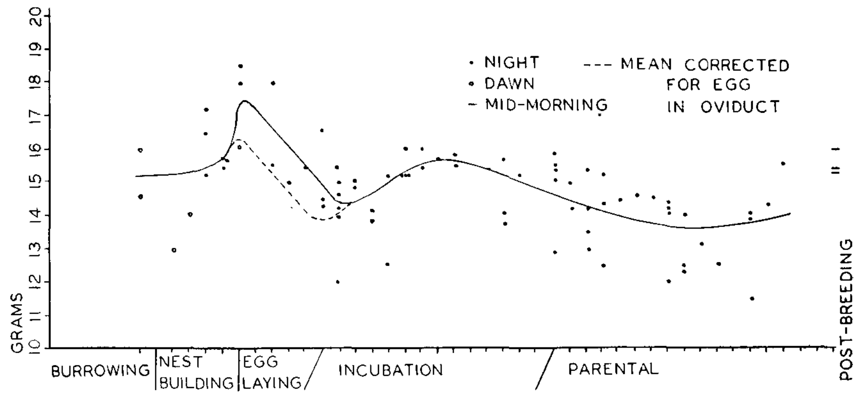

FIG. 12. Body weights of female Bank Swallows. In this and the following figures, the horizontal scale represents the sequence of stages in the breeding cycle.

the total mean weight. (2) During the egg-laying stage and the first day of the incubation phase the female body weight decreased to 14.2 grams. (3) An increase of about 10 per cent during the first half of the incubation period was followed by (4) a gradual decline beginning even before the parental phase. (5) The five specimens collected on the twelfth to fifteenth days of the parental phase suggest the beginning of a return to normal weight. Three individuals collected from post-breeding flocks averaged 15.6 grams (range 15.3–16.0).

The weights of 39 male specimens (Fig. 13) ranged from 11.8 to 16.1 grams with a mean of 13.7 grams, 1.1 grams less than the female body weight. While the difference in body weight between the sexes was greatest at the start of egg laying, females at any stage averaged heavier than males.

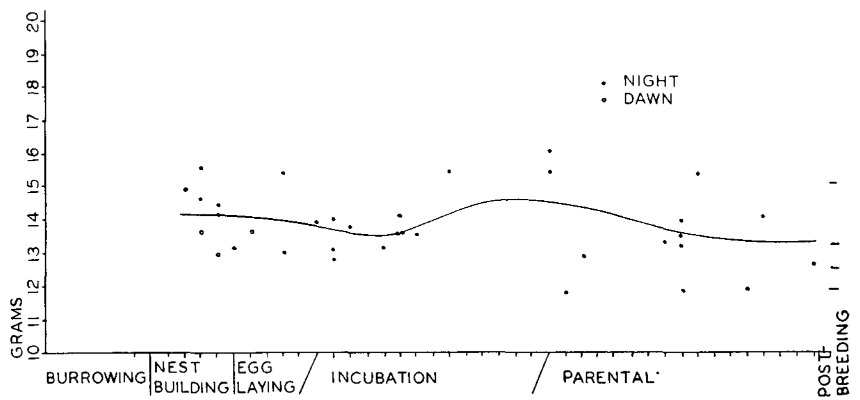

FIG. 13. Body weights of male Bank Swallows.

Fluctuations evident in the weights of males were (1) a slight decrease during nest-building and egg laying, (2) an increase during incubation and (3) a decline during the parental phase. Four post-breeding adult males averaged 13.25 grams (range 11.9-15.2). Nine juveniles collected from a post-breeding flock had a mean weight of 13.2 grams (range 11.6–14.9).

Stoner (1936) analyzed the weights of 249 Bank Swallows, including 22 known females and 13 known males. He reported that females were heavier than males (15.60 and 14.03 grams respectively) and also noted that the average weights declined from May through June and July.

Riddle and Braucher (1931) studied body weight changes during the reproductive cycle in pigeons and doves and found an increase of about eight per cent in weight during incubation. About one-third of this increase occurred in the crop-glands.

Baldwin and Kendeigh (1938) showed that the weights of birds characteristically increase during the day and decrease at night, being lowest at the beginning of each day's feeding activity. In this present study all weights were taken in the evening except a few which were obtained at dawn. These were found to average lower than evening weights during the same stage.

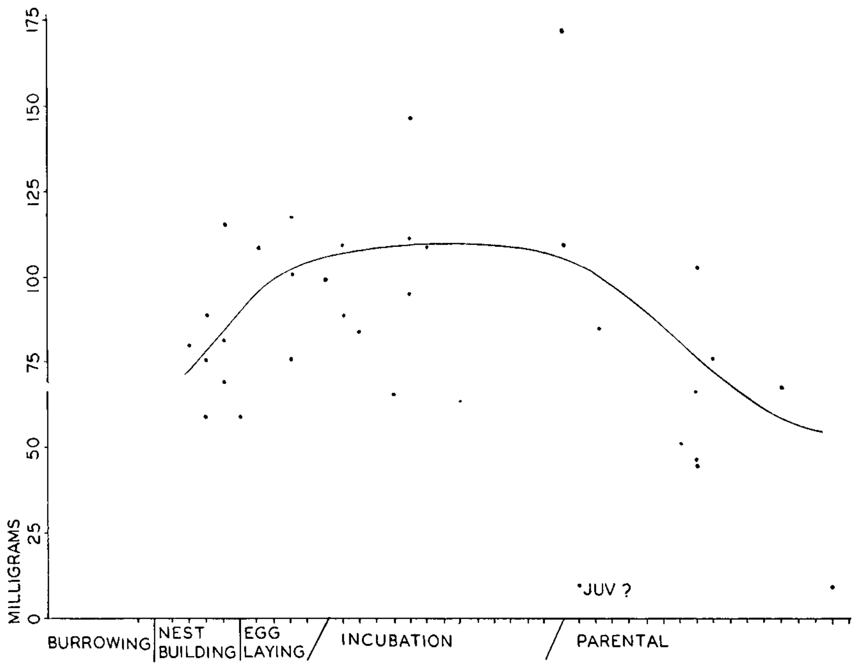

FIG. 14. Bank Swallow testis weights. See text for further explanation.

TABLE 14
BANK SWALLOW TESTIS WEIGHTS

Stage	Frequency	Mean weight	Range (mgm.)
Nest-building	8	78.9 mgm.	59.1–116.1
Egg-laying	4	107.5	80.6–133.5
Incubation	9 (10)	97.3 (87.8)	(2.5) 63.1–147.5
Parental: 1–3	3 (4)	120.0 (92.4)	(9.5) 85.8–163.7
Parental: 8–17	8 (9)	63.4 (57.4)	(9.2) 46.2–103.4

( ) Include three specimens of extremely small size.

TESTES

Weight.—Testes of 35 male Bank Swallows were preserved in fixative and later weighed on a torsion balance. Each of the weights plotted on the graph (Fig. 14) is the average of the two testes of a specimen, except for 10 birds in which one of the testes was used to prepare a smear. At any stage of the breeding cycle a wide range in testes weight was found (Table 14). Three birds had testes much smaller than any other birds so their testes weights (2.4, 9.4, and 9.2 mgm.) are parenthesized in the table.

Histology.—Specimens listed below, representative of each phase of the cycle, were sectioned in paraffin at eight microns and stained in iron hematoxylin and eosin:

Number	*Phase*	*Stage*	*Weight in milligrams*
1.	Nest-building	4	64.2
2.	Egg-laying	3	80.6
3.	Incubation	1	108.4
4.	Incubation	5	134.9
5.	Parental	1	164.5
6.	Parental	3	91.9
7.	Parental	9	44.6
8.	Parental	17	10.7

All of these testes, except no. 8, had bundles of mature sperms around Sertoli cells in the tubules (Stage 7 of Blanchard, 1941). A few free sperms were in the lumens of the seminiferous tubules of specimens from the nest-building and egg-laying stages. In the triangles between tubules large blood vessels and occasional interstitial cells were found. Tubules of incubation and parental stage testes had much greater numbers of free sperm in the lumens. Specimens from the parental stages had increasing amounts of cellular debris. Lumens of the testis from parental stage 9 were quite choked with debris and mature sperms.

Specimen no. 8 appeared to be in an advanced condition of regression. No spermatozoa or spermatids were found in any of the tubules of this testis. Only the basal layer of the tubule epithelium showed any organization and lumens were filled with degenerating cells and cellular debris. The tunica albuginiae and tunicae propriae were several times thicker than any of the other testes sectioned and interstitial cells were relatively more numerous.

Ovary

The ovaries of female Bank Swallows were left *in situ* and preserved in fixative with the whole lower back regions. Later they were dissected, weighed, and examined for the number and size of their ova.

Each of the 79 ovaries collected (from burrowing through parental phases) contained a large number (estimated at from 50 to 60) of white ova of macroscopic size, under 1.5 mm. in diameter. During the four days preceding ovulation from four to six of these ova increased rapidly in size by deposition of yellow yolk. In domestic chickens (*Gallus gallus*) this increase begins 10 days before ovulation (Jull, 1952) and in the Domestic Pigeon (*Columba livia*), about four and one-half days (Riddle, 1916). In the Jackdaw (*Corvus monedula*) the period of rapid increase begins about four days before ovulation (Stieve, in Groebbels, 1937). The enlarged ova showed a distinct gradation in size in each ovary (Table 15). A study of the sequence of sizes together with the presence or absence of an egg in

Table 15
Weights of Ovaries and Sizes of Contained Ova

Specimen number	Stage	Weight of ovary (mgm.)	Size of enlarged ova (dia. in mm.)	Eggs in oviduct	Eggs in Nest
1	B	47.5	–	–	–
2	B	24.0	–	–	–
3	N1	22.0	–	–	–
4	N2	90.8	2, 4	–	–
5	N3	169.5	2, 2, 5	–	–
6	"	186.4	2, 2, 3, 5.5	–	–
7	"	140.0	2, 3, 6	–	–
8	N4	373.0	1.5, 2, 3, 5, 8	–	–
9	"	461.6	6, 8	–	–
10	"	778.3	5, 8, 9	–	–
11	N5	528.8	3, 6, 8	1	–
12	"	462.1	6, 8	1	–
13	"	480.2	3, 6, 8	1	–
14	E2	313.0	8	1	2
15	"	516.8	3, 4, 8	1	2
16	E4	49.6	–	1	3
17	"	40.9	–	1	4
18	E5	37.1	–	–	5
19	"	39.5	–	–	5
20	"	22.4	–	–	4
21–48	Incubation	Mean 31.3 (16.2–52.1)	–	–	3–6
49–79	Parental	Mean 22.4 (6.6–44.1)	–	–	Nestlings

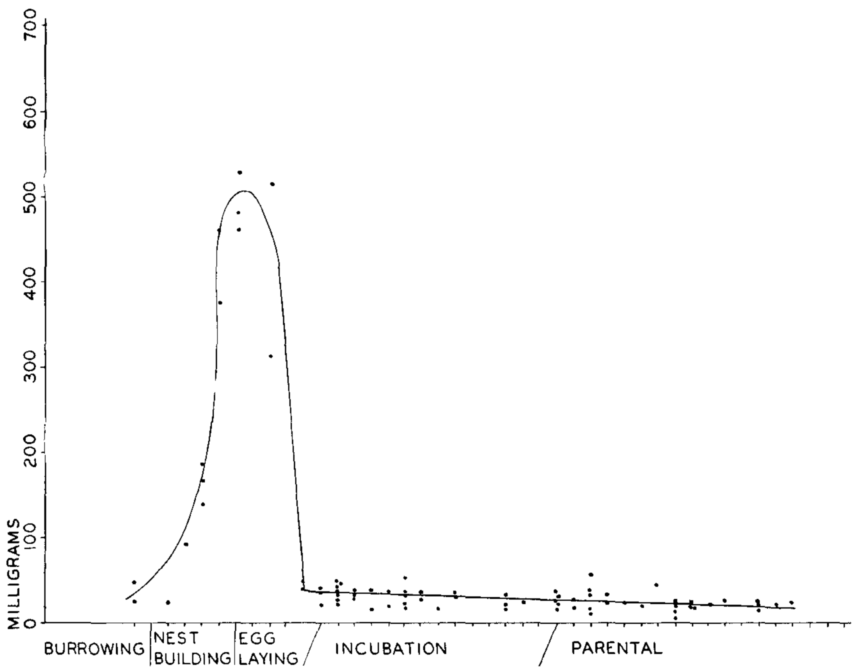

FIG. 15. Bank Swallow ovary weights.

th oviduct indicates that (1) an ovum was two to four mm. diameter on the second day preceding ovulation, (2) four to eight mm. diameter on the day preceding ovulation, and (3) eight or nine mm. diameter at ovulation.

Coincident with the rapid increase in ovum size, the weight of the ovary with ova included increased from about 30 milligrams to over 300 milligrams (Fig. 15). (Seven ovaries containing ova of ovulation size averaged 514.4

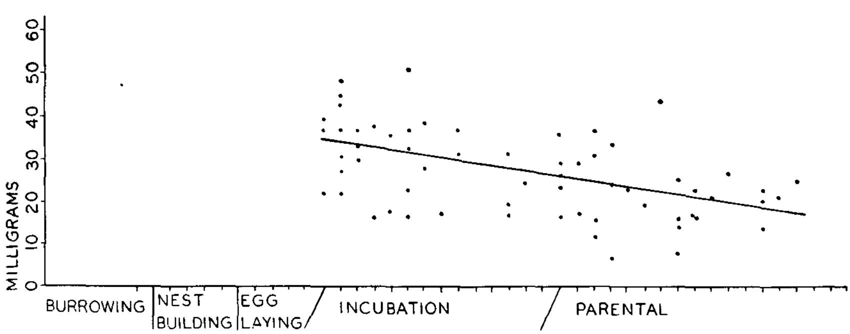

FIG. 16. Bank Swallow ovary weights. Data from specimens taken after egg-laying are repeated here on a greater scale.

mgm.) With the last ovulation the ovary dropped in weight to less than 53 mgm., and looked as it did in the burrowing phase. The appearance of the ovary remained the same throughout the incubation and parental phases, but there was a gradual decline in weight from a mean of 31.3 mgm. in incubation to 22.4 mgm. in the parental phase (Fig. 16).

Oviduct

The curve of oviduct weights (Fig. 17) is very similar to the ovary weight curve. The weight increased very rapidly for about three days before the first ovulation. This increase had probably started slowly some days earlier. By the beginning of ovulation the organs weighed 1500 milligrams. The decline in weight of the oviduct with the last oviposition (to a mean of 366.2 mgm.) is slightly less abrupt than the drop in ovary weight a day earlier. A more gradual decline during incubation reduced the weight to about 50 mgm., a level maintained through the parental phase.

Incubation Patch

The incubation patches of 75 females and the ventral apteria of 14 males were dissected from the freshly killed birds and preserved in Mossman's FAA fixative. Specimens representative of various stages in development or regression of the incubation patch were sectioned at eight microns and stained in iron hematoxylin or Mallory's stain for histological examination.

The four stages in the incubation cycle described by Bailey (1952) for

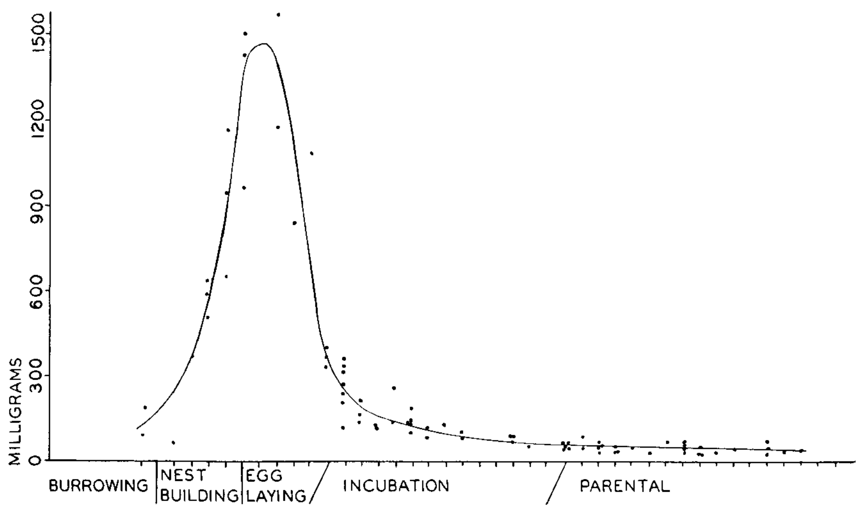

Fig. 17. Bank Swallow oviduct weights. Ova found in the oviducts during the egg-laying phase were removed before weighing.

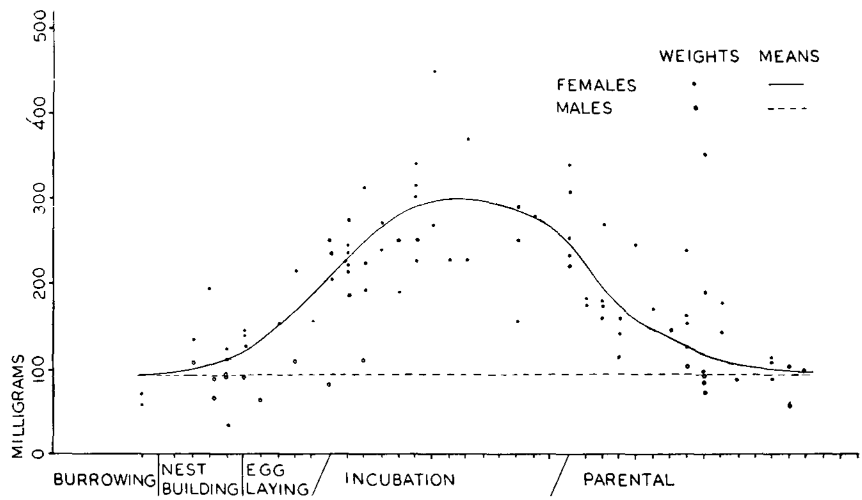

FIG. 18 Bank Swallow incubation patch weights. The open circles represent weights of ventral apteria of males, which do not develop an incubation patch.

the White-crowned Sparrow (*Zonotrichia leucophrys*) are recognized in the Bank Swallow. The following characteristics of each stage should be noted:

Stage I: Defeatherization.—This starts early in the nest-building phase and requires several days, being complete before the first egg is laid. According to Bailey the process is completed in 24 hours in the White-crowned Sparrow and Oregon Junco (*Junco oreganus*).

Stage II: Vascularization.—A remarkable development of the smooth muscle layer of the arteries not noted by Bailey suggests a possible increased development of vasomotor control of these vessels, which deserves further study. Development of such a regulatory mechanism in the incubation patch may have functional significance in conserving body heat while the female is off the egg.

Stage III: Edema.—Distension begins at the time of egg-laying in the lower dermis and as it increases, progresses toward the upper surface until at its maximum the entire dermis is edematous, limited only by a thin upper and basal membrane.

Stage IV: Recovery.—This change begins in the Bank Swallow several days before the eggs hatch, when the edema starts to subside slowly.

Before sectioning, each of the specimens collected was removed from the preserving fluid, rolled carefully on blotting paper to remove any excess of the fluid and weighed on a torsion balance. The weights (Fig. 18) correspond closely to the development and subsidence of edema. The ventral apteria of males underwent none of the changes evident in the females and maintained a uniform weight having a mean of 92.4 mgm. The incubation patches of females developed from apteria of about the same weight, and started to increase in weight during the nest-building phase. They had doubled in weight by the time egg-laying was completed and during the fifth to twelfth

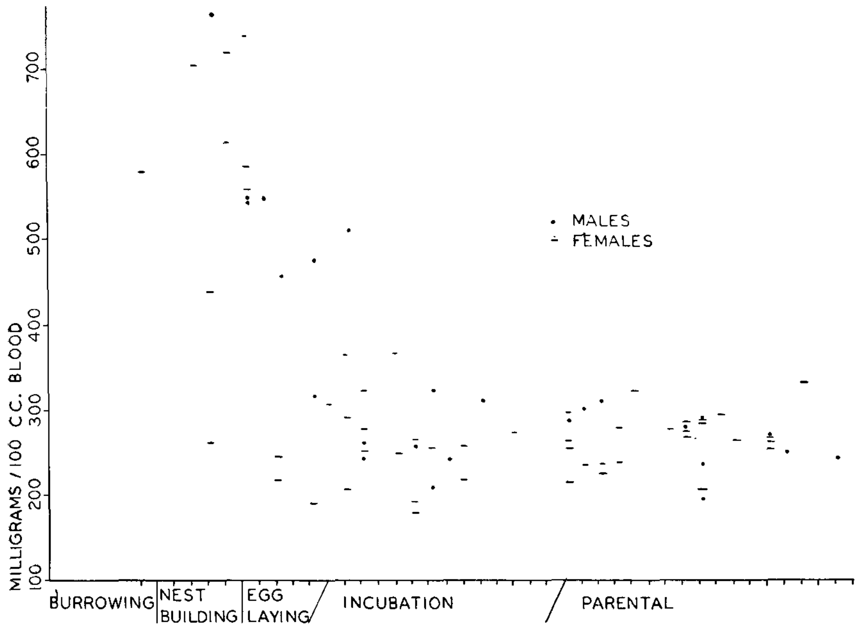

FIG. 19. Blood glucose concentrations in the Bank Swallow. Each symbol indicates the concentration in a single specimen. The mean for each phase of the breeding cycle is graphed in Fig. 20.

days of incubation, maintained a mean maximum weight of 281.0 mgm., about three times the original weight. When hatching began, a decrease in weight had started and by the time the nestlings were two weeks old, the apteria had returned to normal weight.

Blood Glucose

Blood glucose determinations were made by Reinecke's (1942) method on 52 adult females and 25 adult males taken throughout the breeding cycle. The distribution of the individual values obtained are shown in Figure 19.

TABLE 16
BLOOD GLUCOSE CONCENTRATIONS (MGM./100CC.)

Phase in Cycle	Males			Females		
	N	Mean	95 per cent c.l.	N	Mean	95 per cent c.l.
Burrowing........	–	–	–	1	582	–
Nest-building.....	4	601	175	8	579	135
Egg-laying........	4	441	136	4	240	80
Incubation........	7	263	37	15	264	32
Parental..........	10	266	25	24	268	12

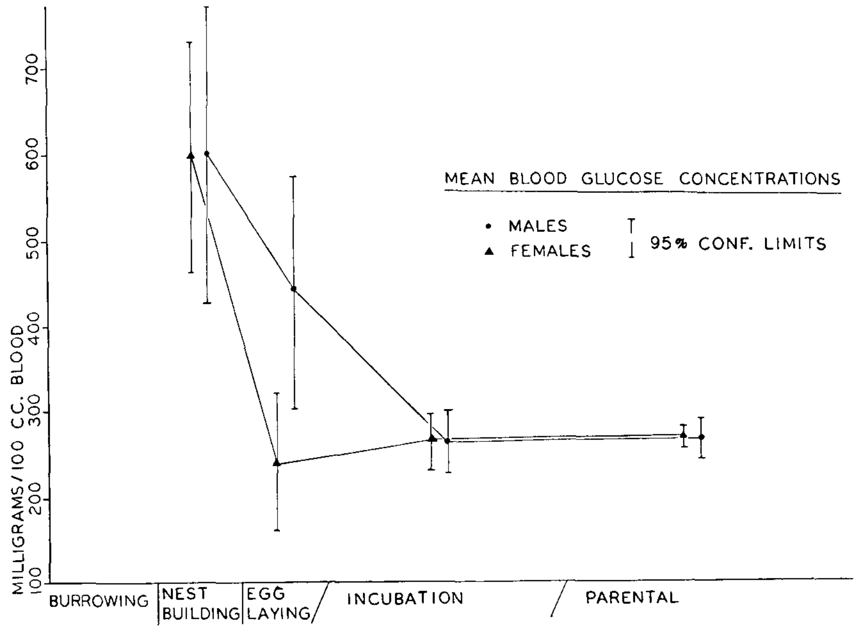

FIG. 20. Mean blood glucose concentrations in the Bank Swallow.

The means for each stage of the cycle are given in Table 16 and are graphed in Figure 20.

During incubation and feeding of young a mean level concentration of 266 mgm./100 cc. was found. Riddle and Honeywell (1924) found that most species of columbiform birds studied had a different and characteristic mean concentration of glucose (from 149 to 258 mgm./100 cc.) and Riddle (1937*b*) found that the concentration for pigeons was maintained at this normal level during incubation and feeding of young. It seems reasonable, therefore, that 266 mgm./100 cc. is the normal concentration for the Bank Swallow.

During the early stages of breeding activity, burrow digging and nest building, there was found in both sexes an elevation of 120 per cent above the level maintained during incubation and feeding of young. From this high the concentration dropped to the normal level quickly in the female and more gradually in the male. It may be conjectured that this striking elevation early in the breeding cycle is related to the high intensity of activity of the birds at that time. It seems probable that the behavior of the birds and the high concentration of blood glucose are both responses to the same hormonal stimuli. Riddle and Honeywell (1923) found a 20 per cent increase in blood sugar of pigeons with each ovulation period, beginning 108

TABLE 17
SERUM CALCIUM CONCENTRATIONS IN THE BANK SWALLOW

Age and Sex	Stage in Cycle	Serum Calcium (m. eq. Ca./l.)
Adult Female	Parental 7	4.9
" "	Parental 8	3.6
" "	Parental 9	3.6
" "	Parental 13	3.4
" "	Parental 14	3.6
" "	Parental 15	3.8
Nestling (undetermined sex)	—	3.6
		Mean....3.8

hours before and maintained at the high level throughout ovulation. The investigations of Riddle (1937) and his associates indicate that the hormonal mechanism of this glycemia is complex. At ovulation in the pigeons a marked hypertrophy of adrenal cortical tissue is found and cortical extracts are shown to moderately increase blood sugar. Prolactin likewise experimentally produces moderate glycemia. Evidence indicates further than an additional substance from the pituitary or adrenal may have a synergistic effect.

The more rapid return to normal apparent in females tested may be due to an increased rate of utilization of glucose associated with other activities including tissue growth in the oviduct and brood patch and deposition of food stores in the eggs by the ovary and oviduct.

SERUM CALCIUM

The method of Sendroy (1942) for photoelectric determination of serum calcium in small quantities of blood was adapted with a modification in the colorimeter filter and light source recommended by W. H. Schaeffer of the Rubicon Company (personal letter). The data obtained are presented in Table 17 but are insufficient for consideration of cyclic changes.

III. CORRELATION OF BEHAVIOR AND PHYSIOLOGICAL CYCLES

A review of the main features of seasonal reproductive cycles in birds seems pertinent before examining the behavior and physiological cycle in the Bank Swallow.

The anterior lobe of the pituitary gland, under the influence of some seasonal environmental factor (such as amount of daylight or temperature) produces gonadotropic hormones which bring the testes and ovaries into breeding condition. In both sexes, two distinct gonadotropic hormones, having separate effects on the gonads, are found. Follicle-stimulating hormone (FSH) brings about growth of ovarian follicles and in the male stimulates development of spermatoza in the seminiferous tubules. An interstitial-cell-stimulating hormone (ICSH or LH) activates the interstitial cells of the testis to secretion of the male sex hormone, testosterone. ICSH is necessary for the production of the female sex hormones by the ovary. The sex hormones have the effects of stimulating development of accessory sex organs and secondary sexual characteristics and of initiating breeding behavior, including taking up of territories, mating, and possibly migration. Physiological effects shown for the female sex hormones, the estrogens, include elevation of calcium, fat, and glucose concentrations in the blood. Large amounts of estrogen have an inhibiting effect on the production of gonadotropins by the pituitary.

Another anterior pituitary hormone directly concerned in avian reproduction is prolactin. The effects of prolactin are initiation of broodiness and maternal behavior. Localized effects demonstrated for this hormone are proliferation of the crop-sac mucosa of pigeons (Riddle, Bates, and Lahr, 1935) and, in synergy with estrogen, the development of the brood patch in fringillids (Bailey, 1952).

The sequence of events in the behavior cycle of the Bank Swallow are brought together in Figure 21 and the factors of the physiological cycle in Figure 22. Physiological factors in the breeding cycle were not measured prior to the nest-building stage, but a brief review of the behavior in this period can be made.

Migration.—Determination of environmental factors effective in inducing migration in the Bank Swallow was not within the scope of this study. Observations were made, however, which indicated that once migration is underway, its rate is correlated with climatic factors. An apparent relationship was seen between time of arrival in the Madison area and temperatures prevailing for the preceding 15 days. Low temperatures may directly inhibit the migratory activity or may impede migration progress indirectly by causing a reduced food supply and necessitating longer periods of feeding. It was noted that activity upon arrival was influenced by weather conditions; fair weather with temperatures near or above normal appear to be necessary for taking up territories and associated behavior leading to pair formation.

Territorial and mating behavior.—On arrival at the breeding grounds the stage of gonadal development of Bank Swallows apparently places them in a disposition to take up territories and to mate.

Territorial behavior centers around a particular burrow. Both members of the pair identify themselves with the chosen site and defend it. The burrow screens much of the activity of the pair from other members of the colony. Thus the actual amount of territorial conflict is reduced, but the attachment to the chosen site is maintained throughout the breeding cycle, and is ex-

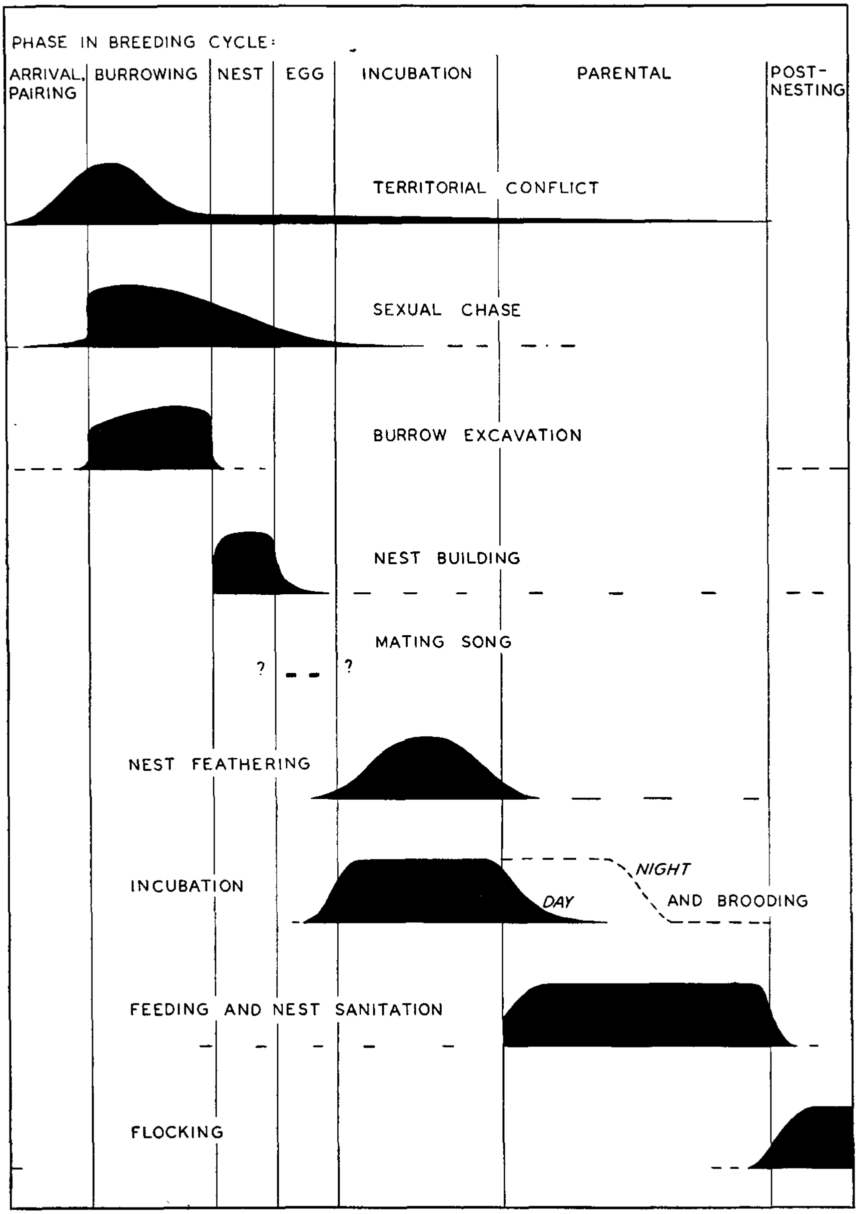

FIG. 21. Summary of behavior elements in the breeding cycle of the Bank Swallow.

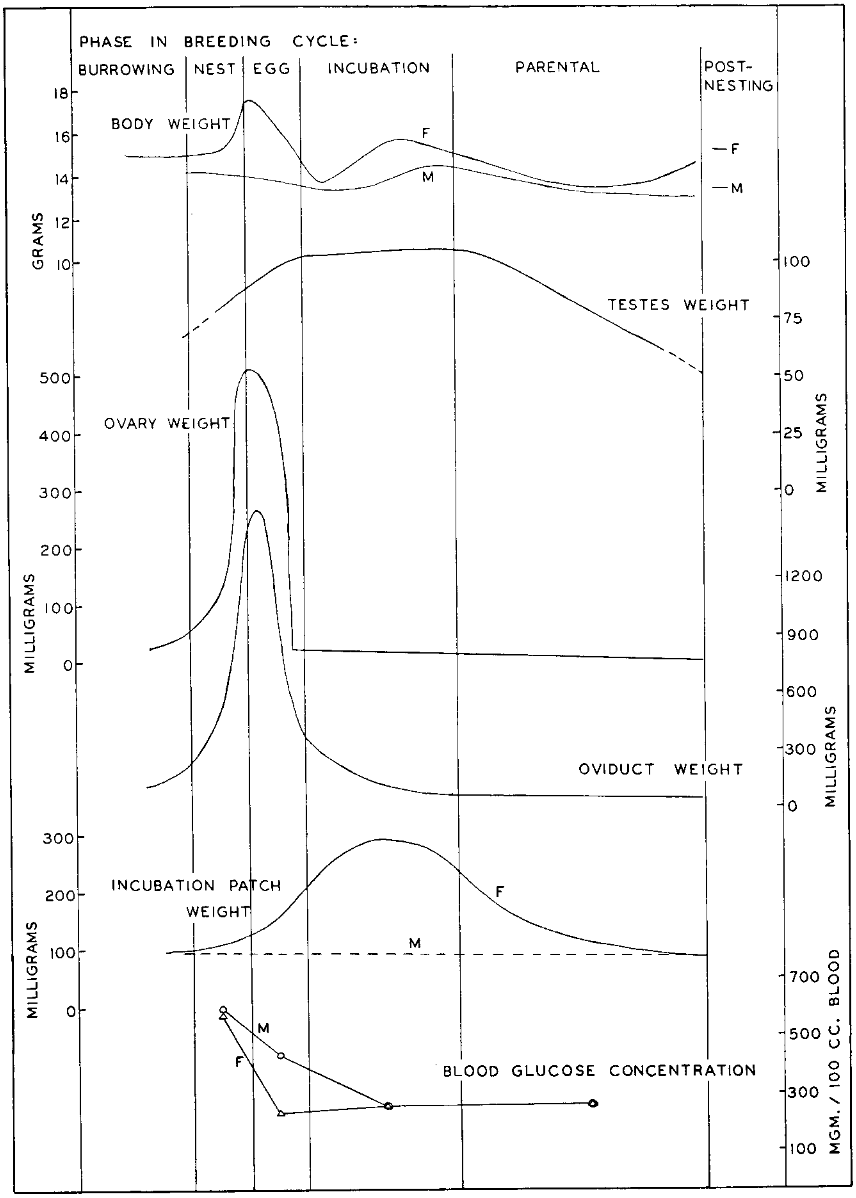

FIG. 22. Summary of physiological factors in the breeding cycle of the Bank Swallow.

pressed by territorial song, threat, or fighting whenever an intrusion occurs. As noted, birds failing to establish territories and obtain mates may leave a colony when breeding gets underway and take up sites in a different place. This also reduces the territorial conflict at the original site.

Mating in various species has been experimentally shown to occur following administration of testosterone in one (Emlen and Lorenz, 1942) or both members of a pair (Noble and Wurm, 1940*b*), or after treatment of one bird with androgen and the other with estrogen (Noble and Wurm, 1940*a*).

Sexual chase in the Bank Swallow is an activity of mated birds. Others join in, but in my observations, do not initiate the chase. This agrees with the findings of R. W. Nero (personal communication) in Red-winged Blackbirds (*Agelaius phoeniceus*). Burrow excavation likewise progresses effectively only after the pair-bond has been formed.

Burrowing and nest-building behavior.—Nest building behavior in the Bank Swallow coincides with the rapid growth of the ovarian follicles. The same correlation has been noted in the pigeon (Riddle, 1916) and Tricolored Red-wing, *Agelaius tricolor,* (Emlen, 1941). In the Bank Swallow nest-building cannot begin until a nest cavity has been excavated, so it seems necessary that some relationship exist between nest-cavity excavation and an internal condition preceding the rapid deposition of yolk. Two possible relationships may be conjectured, either one or both of which may obtain: (1) the activity of burrow and nest-cavity excavation may be motivated by developments which precede *rapid* ovum growth, or (2) excavation and associated behavior activities of the mated pair, such as sexual chase and territory defense, may serve as psychological stimuli for yolk deposition.

Development of the oviduct, as indicated by weight of that organ, follows closely after the ovary increase, but reaches a much higher weight (Note separate weight scales in Fig. 22). Egg production does not reduce oviduct weight as much as ovary weight, but by the end of the incubation period, the oviduct has returned to an inactive condition.

Copulation by mated birds was not observed but probably occurs at least during some part of the nest-building phase. Testes at this time contain large numbers of maturing sperm and relatively small numbers of free sperm in the lumens of the semeniferous tubules, indicating that as spermatozoa mature, they promptly leave the testes. Testes of later stages showed increasing numbers of free sperm in the lumens.

The sharp rise in female body weight in late nest-building can be entirely accounted for by growth of ova and the oviduct. A comparison of the weight of a complete clutch of eggs (7.36 gm. for an average clutch of 5 eggs) with the decrease of ovary weight during five ovulations (about 450 mgm.) and the difference in weight of pre- and post-oviposition oviducts (over 1100 mgm.) indicates that over three-fourths of the material of the eggs is brought into the ovary and oviduct during the period of egg-laying. Relatively little of this comes from other body stores built up in advance, since the post-egg-laying body weight of the female is little lower than her weight before the rapid growth of the ovary.

The slight decline apparent in male body weights through the nest-building and egg-laying phases probably results from the high rate of activity during this period.

The relation of blood glucose concentrations in Bank Swallows to the breeding cycle is obviously not the same as in pigeons in which Riddle and Honeywell (1923) found a 20 per cent increase in blood glucose concentrations of females beginning 108 hours before ovulation and maintained at a high level throughout ovulation, but no change in males. The intense activity apparent in both sexes of the Bank Swallow during the early phases of the cycle indicates an energy utilization distinct from the subdued activity of the domestic pigeon. Some mechanism in the Bank Swallow provides for this need by maintaining blood glucose in both sexes at more than double the usual concentrations. The concentration in egg-laying females returns to an apparently "normal" level. In the incubation and parental phases the blood glucose level is relatively stable in both sexes.

Incubation. In Bank Swallows incubation starts before egg-laying is completed and is the function of both sexes. Incubation and broody behavior have been stimulated in domestic hens by prolactin (Riddle, Bates, and Lahr, 1935). This action of prolactin is accentuated by pre-treatment with sex hormones (Collias, 1946), but is inhibited by a continuing high level of estrogens (Collias, 1940).

Bailey (1952) has shown in fringillids that full development of the incubation patch is due to the combined action of estrogen and prolactin. Estrogen causes vascularization and prolactin causes defeatherization and edema. Stresemann (1934) noted a correlation in many orders of birds between the presence of an incubation patch in either sex and the part played by that sex in incubation. Thus, in most orders, for example Colymbiformes, Procellariiformes, Columbiformes, and Piciformes, both sexes share in incubation and an incubation patch develops in both sexes. In Strigiformes, Falconiformes, and Trochilidae only the females incubate and have incubation patches. In Phalaropes only the males incubate and have patches. Among the passerines the only species in which the male is known to develop an incubation patch is the Clark Nutcracker, *Nucifraga columbiana*, (Mewaldt, 1952). Reasoning that the development of an incubation patch must have functional significance, and that the correlation in most orders between presence of an incubation patch and share of the sexes in incubation must extend also to the Passeriformes, Bailey postulates that male passerines, even where they are known to sit regularly on the eggs, do not incubate. In the Bank Swallow, the male not only sits regularly on the eggs, but in some instances was found to do so at night, and produced a temperature far above the environmental temperature. Development of broody behavior in male Bank Swallows may reflect the presence of prolactin, which in the absence of estrogen fails to produce a brood patch.

Noble and Wurm (1940*b*) found that broody behavior of Black-crowned Night Heron chicks followed treatment with male sex hormone. It is not certain, however, whether this behavior was in response to the testosterone directly or whether the testosterone stimulated the pituitary to secrete prolactin which caused the appearance of the broodiness.

Body-weight in both sexes increases during incubation and begins to decline by the end of that period. The increase may be related to the rather sudden reduction in overall activity in sitting birds. Riddle and Braucher (1931) found that pigeons gain in weight during incubation even though consuming less food per day than at other periods. No data were obtained on the amount of feeding by Bank Swallows during incubation, to determine whether the noted reduction in weight at the end of the incubation period might be related to lowered food consumption.

Feathering of the nest coincides with incubation behavior. Probably the presence of eggs in the nest is an external condition necessary for seeking and carrying feathers to the nest. The variations noted in time and amount of nest feathering may be related to success in finding feathers.

Parental behavior. In Bank Swallows feeding of the young is a response to their own young in the nest or burrow, or later, outside their own burrow. Adults were never seen to feed juveniles other than their own, either in their own or in other burrows. How early in the nestling period they can distinguish their own from other young was not determined.

Emlen (1941) found that male Tricolored Red-wings will feed any young in their own nest at any time after laying has started, but that females will respond only after incubation has started. Emlen (*op. cit.*) and Tinbergen (1939) both noted an incompatibility between sexual and parental activity. This concurs with observations that sexual phases of behavior are under the influence of sex hormones, while parental behavior is induced by prolactin, the effects of which are inhibited by the sex hormones.

Summary

The purpose of this study was to analyse the behavior cycle and certain factors in the physiological cycle of a wild species of bird for correlations that might give insight into conditions that regulate breeding behavior as it occurs under natural conditions.

The Bank Swallow (*Riparia riparia*) was selected as the subject for this study because it breeds in the vicinity of Madison, Wisconsin, in large colonies and the nests are built in burrows from which the birds can be easily obtained.

The arrival dates in the Madison vicinity in the six years 1947–1952 range from April 19 to April 26. Arrival occurred before April 22 in years when the mean temperature of the preceding 15 days was above normal. Arrival was after April 22 when the mean temperature of the preceding 15 days was below normal.

The following sequence of events in pair formation was observed: an unpaired bird (probably the male) selected a burrow site, and defended it by vocal threats and physical force against intrusion. One among those which persistently returned to the defended site eventually was tolerated and became recognized by the bird holding the territory as his mate. Sexual chase and a rarely-heard mating song strengthen the pairing bond. Completed copulations were never observed and are thought to occur within the nest chamber.

Burrows were excavated only by mated birds and both members of the pair shared in the work. Excavation began slowly and erratically in burrow locations where much territorial fighting occurred. Once a burrow is about three inches deep, excavation proceeded at the rate of about five inches a day. A tendency was noted for burrows to be concentrated near the top of the bank. A positive correlation was found between amount of sand in the soil and burrow depth.

The nest chamber was usually supplied with a mat of grass, straw or roots before egg-laying began. A lining of feathers was added after the eggs were laid. Nesting materials were brought by both members of the pair.

Eggs were laid at the rate of one per day. No instances of second nestings were found in this study, but re-nestings following nest destruction were common. Mean size of first clutches was 5.0 eggs. Later clutches, believed to be re-nestings, averaged 4.0 eggs.

Incubation usually began one or two days before the clutch was completed. Contrary to generalizations made for passerine birds, males shared in incubation. An incubating male was found to raise the temperature of the eggs to 96°F., as much as 21°F. above the temperature of the unincubated nest. In two instances the male alone was found at night on nests containing eggs. The incubation period under natural conditions was found to be 15 days. Nestlings were brooded almost constantly on the day of hatching, but the amount of daytime brooding decreased rapidly during succeeding days. Both of the parents or either alone brood young nestlings at night, but the parents were rarely found at night in burrows containing nestlings over 12 days old.

Nest sanitation was maintained throughout the nestling period. The mean hourly feeding rate found in 33 nest-hours of observation in fair weather was 24.7 feedings per nest. The feeding rate was not proportionately greater in larger broods so that the number of feedings per nestling was greater in smaller broods. Males fed the nestlings more frequently than did females. After 12 days of age nestlings are frequently fed at or near the entrance to the burrow. Observation of individually-marked parents feeding nestlings having colored leg bands designating their home burrow indicated that Bank Swallows can distinguish their own nestlings from others, and will feed only their own nestlings, even when they have left their own burrow and returned to the same or another burrow. The nestlings may fly from the burrow as early as 18 days if disturbed, but usually took their first flight at about 23 days of age. In several instances the young birds were lured from the nest by reduced feeding and by calling of the parents.

Abortive burrowing and nest-building was shown by post-breeding flocks of juveniles and adults.

Data on the morphological and physiological cycles were obtained from 79 females and 35 males collected from their burrows at night, together with the nest contents from which the stage of the birds was determined.

The mean body weight of females (14.8 grams) increased with growth of the ovarian follicles and oviduct preceding ovulation, decreased with egg-laying, rose during the first half of incubation, then declined again to the end of the breeding cycle. Mean weight of males (13.7 grams) showed a similar rise and decline in incubation and parental phases.

Testes were heaviest through the incubation period. Regression started early in the parental phase and in a specimen from the seventeenth day of the parental phase, an advanced condition of regression was found.

Ovaries increased tenfold in weight during the four days preceding the first ovulation. Ova were eight or nine millimeters in diameter when ovulation occurred. Oviduct weights increased at the same time as ovary weights and reached a peak of 1500 milligrams at the time of the first ovulation.

A study of the histological and weight changes in development and regression of the incubation patch in females indicated that defeatherization started in early nest-building and required several days; vascularization produced a remarkable development of the smooth muscle layer of the arteries. The weights corresponded closely to the increase and subsidence of edema. No such changes occurred in the ventral apteria of males.

During nest-building blood glucose concentrations of both sexes were more than double the normal level of 266 mgm./100 cc. found during incubation and parental phases.

Correlations between elements of the behavior and physiological cycles were noted and discussed and comparisons made with data on other species of birds.

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